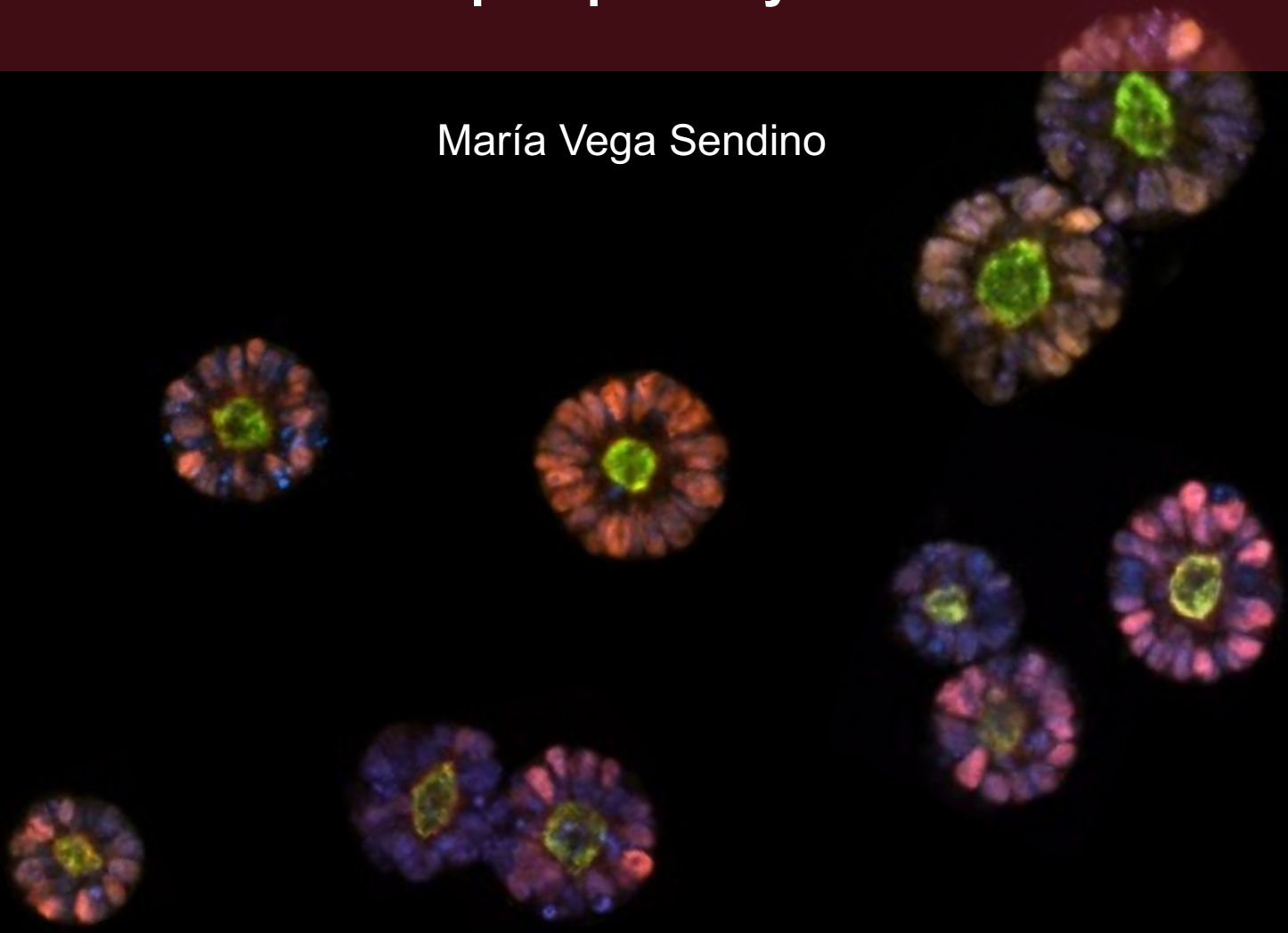
Universidad Autónoma de Madrid

Programa de Doctorado en Biociencias Moleculares

# Exploring the role of the ETS transcription factor ERF during the transition from naïve to primed pluripotency

María Vega Sendino



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Universidad Autónoma de Madrid

Facultad de Ciencias

Departamento de Biología Molecular

# EXPLORING THE ROLE OF THE ETS TRANSCRIPTION FACTOR ERF DURING THE TRANSITION FROM NAÏVE TO PRIMED PLURIPOTENCY

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BS in Biology

MS in Biotechnology

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**Dr. Sergio Ruiz Macías**, Stadtman Investigator in the Laboratory of Genome Integrity at the National Institutes of Health (NIH)

CERTIFIES:

That the Doctoral Thesis entitled: "**Exploring the role of the ETS transcription factor ERF during the transition from naïve to primed pluripotency**", developed by **Ms. María Vega Sendino, BS, MS** meets all the requirements to obtain the **Doctor of Philosophy (PhD) in Molecular Biology** and that it will be defended at the Universidad Autónoma de Madrid with the aforementioned objective. This thesis has been carried out under my direction and I authorize its presentation to the Tribunal.

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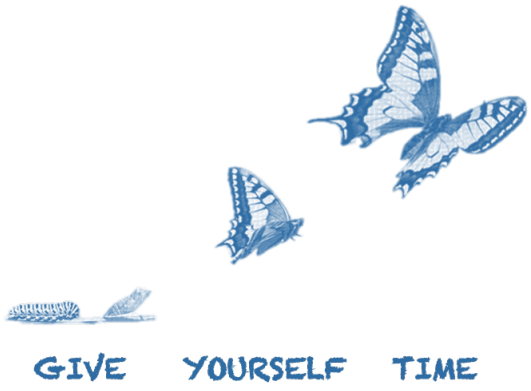

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# RESUMEN

El embrión preimplantacional es un excelente modelo *in vivo* para estudiar los cambios en plasticidad durante el desarrollo y la especificación celular. Las células embrionarias del epiblasto, germen del futuro embrión, se consideran pluripotentes ya que tienen el potencial de generar todos los tipos celulares del organismo. El estado de pluripotencia en el que se encuentra el epiblasto preimplantacional, previo a cualquier especificación, se define generalmente como "*naïve*". Sin embargo, a medida que el embrión crece y se desarrolla después de implantarse, las células del epiblasto adquieren cierto grado de especificación, aunque siguen siendo pluripotentes. Este estado de pluripotencia asociado al epiblasto post-implantacional se define como "*primed*". Aunque la transición de un estado pluripotente *naïve* a *primed* está bien caracterizada, los reguladores finales de las vías de señalización implicadas en este proceso (FGF, WNT y TGF/BMP) se desconocen en su mayoría. En particular, a pesar de la relevancia de la vía FGF/MAPK y su papel en promover la salida del estado *naïve* de pluripotencia, poco se sabe acerca de cómo la señalización mediada por FGF silencia el programa transcripcional del estado *naïve* y facilita la transición al estado *primed* de pluripotencia.

En esta Tesis, para analizar los mecanismos moleculares que coordinan la transición del estado de pluripotencia *naïve* a *primed*, hemos utilizado un modelo celular genético en ESC (*embryonic stem cells* o células madre embrionarias) deficiente en todas las proteínas RAS. Esto nos ha permitido diseccionar molecularmente el papel de los reguladores finales de la vía FGF/MAPK. Nuestros resultados demuestran que las células madre embrionarias $RAS^{KO}$ diferenciadas permanecen atrapadas en un estado intermedio de pluripotencia con características asociadas a *naïve* y a *primed*. La eliminación del factor de transcripción ERF permite salir a las células deficientes en RAS del bloqueo en este estado intermedio de pluripotencia. Mecanísticamente, ERF se une a *super-enhancers* específicos de las ESC para garantizar un nivel de expresión óptimo de los factores de transcripción asociados a un estado de pluripotencia *naïve*, incluido NANOG. De esta manera, ERF protege a las ESC de diferenciar prematuramente en ausencia de la señalización mediada por FGF. Tras la activación de la vía de FGF/MAPK, ERF se libera de la cromatina, un evento que es necesario y suficiente para desencadenar el silenciamiento de los genes *naïve* y la completa transición al estado de pluripotencia *primed*. Finalmente, hemos observado que ERF controla la metilación de sitios CpG durante la transición a *primed* regulando negativamente la expresión de la *de novo* metiltransferasa DNMT3B a través de LIN28.

En conjunto, en este trabajo proporcionamos información detallada y novedosa sobre cómo ERF controla la vía FGF/MAPK en ESC de ratón. En conjunto, nuestros resultados demuestran cómo ERF impone un nivel exquisito de coordinación durante la transición de pluripotencia *naïve* a *primed* a diferentes niveles.

# ABSTRACT

The pre-implantation embryo is an excellent *in vivo* resource to study changes in developmental potential and cell fate specification. Embryonic cells from the epiblast are pluripotent as they have the potential to generate all cell lineages of the organism. The state of pluripotency found in the pre-implantation epiblast, prior to any lineage specification, is usually defined as naïve. However, as the embryo expands and develops after implantation, epiblast cells become individually fated, although still retain pluripotent features. This state of pluripotency associated to the post-implantation epiblast is defined as primed. Although the transition from naïve to primed pluripotency has been well characterized, the downstream regulators of the signaling pathways involved in the process (FGF, WNT and TGF/BMP), remain mostly unknown. In particular, despite the relevance of the activation of the FGF/MAPK pathway and its role in promoting the exit from naïve pluripotency, little is known about how FGF signaling silences the naïve pluripotent transcriptional program and facilitates the transition to a primed pluripotent state.

In this Thesis, we examined the molecular mechanisms coordinating the naïve to primed transition by using a RAS-deficient genetic cell model, which allowed us to specifically dissect the role of downstream regulators of the FGF/MAPK pathway. Our results show that differentiated $RAS^{KO}$ ESC remain trapped in an intermediate state of pluripotency with naïve-associated features. Elimination of the transcription factor ERF overcomes the developmental blockage of RAS-deficient cells from this intermediate state. Mechanistically, ERF binds to ESC super-enhancers to ensure optimal expression level of naïve pluripotent transcription factors, including NANOG, and shields ESC from premature commitment in the absence of FGF signaling. Moreover, we determined that upon activation of FGF/MAPK signaling ERF is released from chromatin, an event that is necessary and sufficient to trigger the decommission of naïve enhancers and the full transition to primed pluripotency. Finally, we found that ERF controls CpG methylation during the transition to primed pluripotency by regulating negatively the expression of the *de novo* methyltransferase DNMT3B through LIN28 regulation.

Collectively, in this Thesis work we provide detailed and novel mechanistic insights on how ERF controls the FGF/MAPK pathway in ESC. Indeed, our findings revealed how ERF imposes an exquisite level of coordination during the transition from naïve to primed pluripotency at different levels.

# ABBREVIATIONS

| | |
|---|---|
| ATAC-seq | Assay for Transposase-Accessible Chromatin sequencing |
| A.U. | Arbitrary Units |
| CDK8/19i | Cyclin Dependent Kinase 8 and 19 inhibitors |
| CRISPR | Clustered Regularly Interspaced Short Palindromic Repeats |
| CUT&RUN | Cleavage Under Targets and Release Using Nuclease |
| deGFP | Destabilized Enhanced Green Fluorescent Protein |
| DOX | Doxycycline |
| DPPA3 | Developmental Pluripotency Associated 3 |
| E | Embryonic post-fertilization day |
| EGF | Epidermal Growth Factor |
| ELK1 | ETS LiKe 1 |
| EPI | Epiblast |
| EpiLC | Epiblast-Like Cells |
| EpiSC | Epiblast Stem Cells |
| ERF | ETS2 Repressor Factor |
| ERK | Extracellular signal-regulated Kinases |
| ESC | Embryonic Stem Cells |
| ETS | E26 transformation-specific |
| ETV | ETS Translocation Variant |
| FA | Fibroblast Growth Factor 2 + Activin-A |
| FAX | Fibroblast Growth Factor 2 + Activin-A + XAV939 |
| FGF | Fibroblast Growth Factor |
| FGFR | Fibroblast Growth Factor Receptor |
| FSC | Formative Stem Cells |
| GAP | GTPase-Activating Protein |
| GDP | Guanosine Diphosphate |
| GEF | Guanine nucleotide Exchange Factor |
| GTP | Guanosine Triphosphate |
| H3K27ac | Histone H3 Lysine 27 Acetylation |
| hCG | Human Chorionic Gonadotropin |
| ICM | Inner Cell Mass |
| IF | Immunofluorescence |
| IU | International Unit |
| IVF | *In Vitro* Fertilization |

| | |
|---|---|
| LIF | Leukemia Inhibitory Factor |
| MAPK | Mitogen-Activated Protein Kinase |
| mRNA | Messenger RNA |
| OHT | 4-Hydroxytamoxifen |
| PC | Principal Component |
| PCA | Principal Component Analysis |
| PDX | Podocalyxin |
| PEA3 | Polyoma Enhancer Activator 3 |
| PGC | Primordial Germ Cells |
| PGC-LC | Primordial Germ Cell Like Cells |
| PMSG | Pregnant Mare's Serum Gonadotropin |
| PRDM14 | PR-domain-containing 14 |
| PrE | Primitive Endoderm |
| RBPJ | Recombination Signal Binding Protein for Immunoglobulin Kappa J Region |
| RNA | Ribonucleic Acid |
| RNA-seq | RNA sequencing |
| RRBS | Reduced Representation Bisulfite Sequencing |
| RSC | Rosette-like Stem Cells |
| sgRNA | Single Guide RNA |
| TCF3 | Transcription Factor 3 |
| TE | Trophectoderm |
| TGF-β | Transforming Growth Factor β |
| TSC | Trophoblast Stem Cells |
| WB | Western Blot |
| WNT | Wingless-related Integration Site |
| XPSC | Chimera Pluripotent Stem Cells |
| ZGA | Zygotic Genome Activation |
| 2i | 2 inhibitors: MEK inhibitor + Glycogen Synthase Kinase-3 inhibitor |
| 2iL | 2i + LIF |
| 5mC | 5-MethylCytosine |

# INTRODUCTION

## Early mouse embryonic development

Pre-implantation mouse embryonic development is a complex and fascinating process that extends from egg fertilization to the implantation of the blastocyst in the uterus (Figure 1). The blastocyst is a self-organized complex structure consisting of a hollow sphere of cells with an outer polarized epithelium (trophectoderm, TE) enclosing a group of cells known as the inner cell mass (ICM) (Saiz and Plusa, 2013, Yao et al., 2019). The ICM further differentiates into a monolayer of epithelial cells (primitive endoderm, PrE) and the epiblast (EPI). The TE and PrE will derive the extra-embryonic cell types (placenta and yolk sac) whereas the EPI will give rise the entire fetus (Rossant, 2018, Pfeffer, 2018, Chazaud and Yamanaka, 2016). This complex process has been extensively used as a model for studying the mechanisms underlying developmental decisions and cell fate transitions (Rossant, 2018, Pfeffer, 2018, Chazaud and Yamanaka, 2016).

The onset of embryonic development starts with the fusion of the gametes, an oocyte and a sperm (Figure 1). Each of the gametes carry one set of chromosomes and when fused, the diploid set of chromosomes in the single cell embryo or zygote, is established. The zygote holds the state of maximum developmental cell plasticity, defined as totipotency, and has the ability to generate all cell types, including embryonic and extra-embryonic tissues (Lu and Zhang, 2015). After fertilization, the zygote undergoes a series of cleavage divisions and generates an increased number of smaller cells, known as blastomeres, without substantial change in the size of the embryo, in 2-cell, 4-cell and 8-cell embryos, consecutively (Figure 1). Although these first divisions are essentially driven by maternally deposited mRNA efficiently translated after fertilization, new transcripts need to be synthesized from the zygotic genome (Sha et al., 2019). Zygotic RNA expression starts as an initial burst at the end of the one-cell stage followed by a second larger burst at the end of the two-cell stage (Jukam et al., 2017, Eckersley-Maslin et al., 2018, Schulz and Harrison, 2019). The transition from maternal to zygotic transcription is a process known as zygotic genome activation (ZGA) and it is the first critical process that will determine the successful subsequent development.

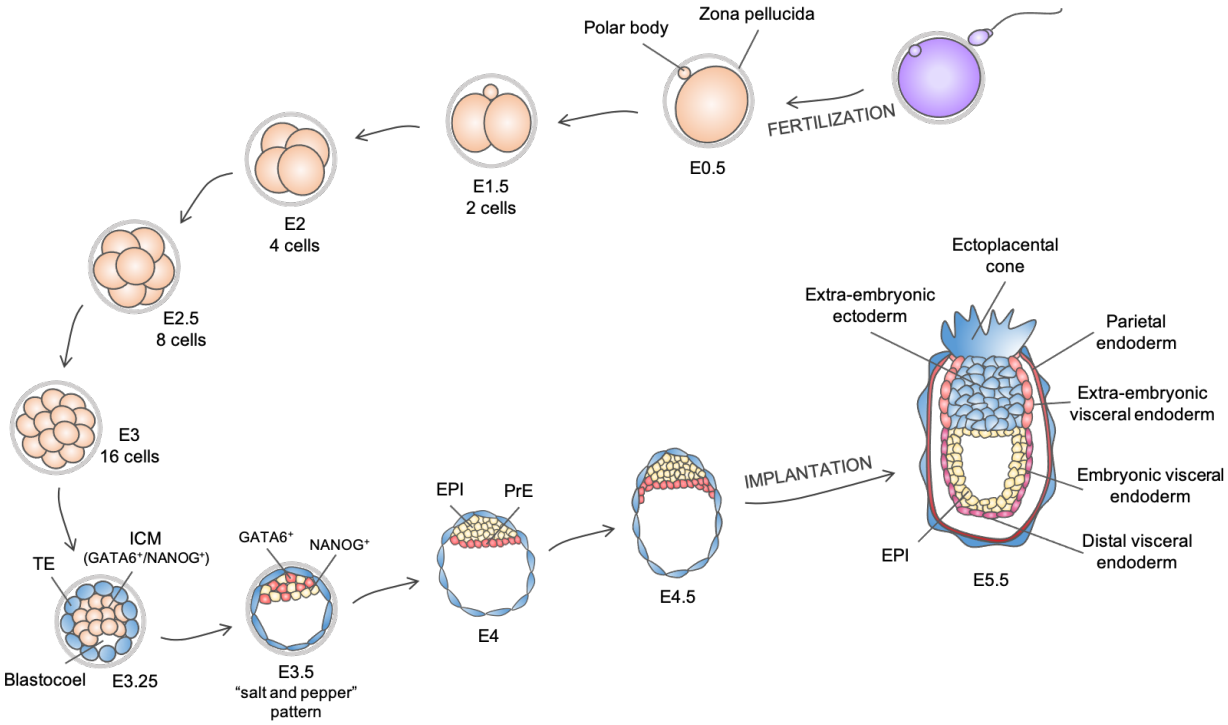


**Figure 1. Stages of mouse pre-implantation development.** The temporal sequence of events during pre-implantation mouse embryo development with relevant embryonic stages and cell lineages generated as a result of the first and the second cell-fate decisions is shown in this schematic representation.

Similar to the zygote, the blastomeres at the two-cell embryo are also considered to be totipotent. This unlimited potential becomes progressively more restricted as the embryo develops. At the 8-cell stage, cell compaction within the embryo is the mechanical signal that induces the first lineage decision, specifying the TE and the ICM, creating the embryonic structure commonly referred to as the morula (Figure 1). Different elements, such as cell polarity, cell position, mechanical forces and metabolism, affect the first cell fate decision. Indeed, differential Hippo signaling leads to a mutually exclusive expression pattern of the transcription factors CDX2 and SOX2, which will specify TE and ICM, respectively (Saiz and Plusa, 2013, Yao et al., 2019). ELF5, EOMES, GATA3 and other transcription factors participate in the maturation and specification of the different cell types arising from the TE (Sasaki, 2010) whereas OCT4, ESRRB, NANOG, KLF2/4/5 and others act together to regulate a network of genes, including themselves, to support the pluripotent stem cell state of the ICM (Li and Izpisua Belmonte, 2018).

By definition, the term “morula” includes embryos at different stages spanning from the compacted 8-cell embryo to the developmental point prior to blastocyst formation at the 32-cell stage. During blastocyst formation, the cells from the ICM differentiate into either EPI or PrE (Figure 1). This second cell fate decision also involves the reciprocal expression of specific transcription factors. By the embryonic day 3.5 (E3.5), all cells from the ICM co-express the EPI marker NANOG and the PrE marker GATA6 (Bessonnard et al., 2014). Soon after that, their expression becomes mutually exclusive within the ICM, resulting in what is known as a “salt and pepper” pattern of single $GATA6^+$ and $NANOG^+$ cells. Single $GATA6^+$ cells will migrate and establish a single layer of cells in contact with the blastocoel, the fluid-filled cavity characteristic of the blastocyst englobing the $NANOG^+$ cells from the EPI (Figure 1). In the mouse embryo, the EPI/PrE lineage cell decision is determined by the fibroblast growth factor (FGF) signaling activity through the RAS/MAPK pathway (Yamanaka et al., 2010) (see below). By not a well understood mechanism, FGF4 as well as FGFR (FGF receptor) I and II are differentially expressed within the cells of the ICM generating a stochastic gradient of RAS/MAPK activity, critical to specify PrE (Yamanaka et al., 2010). In fact, mutations in FGF4 or its receptors (FGFRI and FGFRII) leads to the absence of PrE formation and the blockage on the EPI state (Kang et al., 2013, Kang et al., 2017, Kunath et al., 2007). Conversely, over-activation of the RAS/MAPK pathway drives the cells from the ICM toward a PrE fate at the expense of the EPI (Yamanaka et al., 2010). Therefore, by modulating FGF signaling, PrE- and EPI-progenitor cells could still shift towards the other alternative fate, suggesting that the ICM cells are not fully committed to their final fate during blastocyst formation (Yamanaka et al., 2010). Furthermore, FGF signaling is not necessary for later aspects of PrE progression, but it is essential for the maturation of the EPI cells, promoting their transition from naïve to primed pluripotency (Nichols and Smith, 2009, Kunath et al., 2007).

## Naïve and primed pluripotency and what is in between

The cells residing within the ICM are considered to be pluripotent as they have the potential to generate all cell lineages of the mature organism. This state of pluripotency found in the pre-implantation epiblast, prior to any lineage specification, is usually defined as naïve (Wray et al., 2010, Nichols and Smith, 2012, Weinberger et al., 2016, Nichols and Smith, 2009). However, as the embryo expands and develops after implantation, epiblast cells become individually fated although still retaining pluripotency features. This state of pluripotency

associated to the post-implantation epiblast is defined as primed (Nichols and Smith, 2012, Nichols and Smith, 2009, Wray et al., 2010, Weinberger et al., 2016). More than distinct pluripotent states, naïve and primed, they can be viewed as different phases of a coordinated developmental progression where naïve unbiased cells mature responding to inductive cues to initiate a multi-lineage decision commitment (Smith, 2017).

## Capturing naïve and primed pluripotency *in vitro*

Mouse embryonic stem cells (ESC), *in vitro* counterparts of the pre-implantation epiblast, represent a unique system to study the molecular mechanisms underlying the acquisition and maintenance of pluripotency and self-renewal. Important discoveries made possible in the early 80's the isolation and culture of ESC from the ICM of developing pre-implantation mouse embryos (Evans and Kaufman, 1981, Martin, 1981). These cells are defined by an unlimited self-renewal capacity while retaining the attributes of pre-implantation epiblast identity and potency. A key signal for promoting self-renewal and maintaining pluripotency of ESC is the IL6-family cytokine leukemia inhibitory factor (LIF), which activates STAT3 and suppresses differentiation by impairing MAPK activation (Williams et al., 1988). Indeed, *in vitro* culture in the presence of two small molecule inhibitors (2i), which suppress the MEK pathway (MEKi) and glycogen synthase kinase-3 (GSK3βi, a WNT pathway agonist), is sufficient to stabilize and sustain ESC in naïve conditions (Table 1) (Ying et al., 2008). ESC under these conditions resemble cells in the ICM of embryos at E3.5-E4.25.

However, as mentioned before, pluripotency is not a blunt term that embraces a unique and defined cellular state. In fact, it is possible to establish cultures of pluripotent cells from post-implantation embryos using culture conditions without LIF but including FGF (activating MAPK pathway) and Activin A (member of transforming growth factor-β familiy, TGF-β) (Tesar et al., 2007, Brons et al., 2007). These cells are epiblast stem cells (EpiSC) and retain the alternative pluripotent state, referred as primed pluripotency (Table 1). Mouse EpiSC are developmentally similar to the ectoderm of late-gastrula embryo and display anterior primitive streak properties found in post-implantation embryo at E6.5-E7.5 (Tesar et al., 2007, Brons et al., 2007).

## Transcriptional changes during naïve to primed transition

The transition from naïve to primed pluripotency correlates with a dramatic morphological transformation, accompanied by dynamic transcriptional and epigenetic changes (Brons et al., 2007, Nichols and Smith, 2009, Tesar et al., 2007). Indeed, the gene regulatory network that sustains naïve pluripotency is well characterized. In addition to the core pluripotent transcription factors, OCT4 and SOX2, an accessory set of transcription factors, including NANOG, KLF4, REX1 and TBX3 among others, are differentially expressed in naïve ESC and pre-implantation epiblast sustaining the naïve pluripotent state of ESC. However, these naïve factors are downregulated in EpiSC as well as in the post-implantation epiblast (Boroviak et al., 2015). Following this downregulation, the post-implantation transcriptional regulatory network takes place to support primed pluripotency. In this case, a set of different transcription factors or epiblast-specific genes, including OTX2, FGF5 and OCT6, are upregulated (Kalkan et al., 2017). Of note, these two pluripotent cell types are interconvertible by modifying the culture conditions or expressing specific transcription factors (Weinberger et al., 2016).

## An extensive *de novo* DNA methylation during naïve to primed transition

In addition to the dramatic transcriptional change, naïve ESC and pre-implantation epiblast also undergo extensive *de novo* methylation during their transition toward a primed state and upon implantation (Kalkan et al., 2017, Seisenberger et al., 2012, Auclair et al., 2014). Indeed, global demethylation resulting from epigenetic reprograming takes place after fertilization. During early embryonic development, the levels of methylation are slowly restored, especially after the exit from naïve pluripotency. In fact, hypomethylated naïve cells undergo extensive DNA methylation during the transition to primed pluripotency due to the upregulated expression of *de novo* methyltransferases DNMT3A and DNMT3B (Boroviak et al., 2015, Kalkan et al., 2017).

The expression of the DNMT3A and DNMT3B methyltransferases is regulated by PRDM14 (PR-domain-containing 14), which represses the expression of several genes, including DNMT3, by recruiting PRC2 (Polycomb repressive complex 2) to their promoters (Figure 2) (Yamaji et al., 2013). Initially, PRDM14 was identified as a critical regulator during the specification of primordial germ cells (PGC) from the epiblast (Yamaji et al., 2008) and,

subsequently, it was found to maintain naïve pluripotency by repressing FGF signaling as well as the expression of DNMT3 proteins (Yamaji et al., 2013). In addition, the expression of DNMT3 proteins is also regulated indirectly by the LIN28A/B proteins (Figure 2). LIN28A/B are well-known RNA-binding proteins that repress the maturation of the let-7 microRNA family. Functionally, let-7 targets a number of mRNA transcripts for degradation including those of DNMT3A and DNMT3B (Balzeau et al., 2017). Additionally, DPPA3 (Developmental Pluripotency Associated 3, or Stella), expressed in pre-implantation embryos and during PGC specification (Saitou et al., 2002, Sato et al., 2002), has also been implicated in preventing excessive DNA methylation by sequestering the E3 ubiquitin ligase UHRF1 (Du et al., 2019). Importantly, DPPA3 is downregulated by DNMT3-mediated promoter methylation as a key event during the naïve to primed transition (Sang et al., 2019). Lastly, DNMT3L is another member of the DNMT3 family which lacks enzymatic activity and interacts with DNMT3A/B to enhance their catalytic activities *in vitro* and thus, regulates *de novo* DNA methylation (Veland et al., 2019). Collectively, the control mediated by different proteins over the levels of methylation during the transition from naïve to primed pluripotency highlights the relevance of this process.

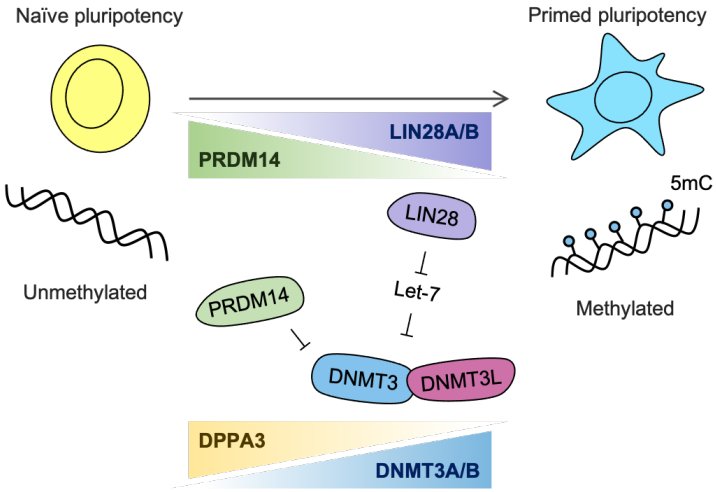


**Figure 2. Regulation of the DNMT3 proteins.** In naïve pluripotent ESC, the expression of DNMT3 is repressed by PRDM14 as well as by the Let-7 microRNAs. In primed pluripotent ESC, PRDM14 and DPPA3 are down-regulated and LIN28 represses the activity of Let-7 microRNAs, allowing the expression of DNMT3 proteins and the consequent *de novo* DNA methylation. DNMT3L interacts with DNMT3A/B to enhance their catalytic activities.

## *In vitro* models to study the transition from naïve to primed pluripotency

During the last decade, different pre- to post-implantation *in vitro* models using mESC have been developed, allowing the characterization of the cellular and molecular changes that take place during this important transition (Buecker et al., 2014, Bedzhov and Zernicka-Goetz, 2014, Hayashi et al., 2011, Nakaki et al., 2013).

In a first model, differentiation to transient epiblast-like cells (EpiLC) from ESC grown in naïve conditions can be accomplished *in vitro* by using FGF2 and Activin A (FA hereafter), the same cytokines that are required for the derivation of EpiSC (Figure 3). EpiLC are difficult to maintain *in vitro* since they undergo extensive cell death two days after induction, which suggest that they require different conditions for their maintenance (Hayashi et al., 2011). Importantly, the derivation of EpiLC have historically been used as starting point for further differentiation toward PGC, an ability that is absent in naïve ESC and EpiSC. This indicates that only cells from the epiblast at E5.5-E6.0 are efficient precursors for PGC specification prior to EpiSC specification (Ohinata et al., 2009).

In a second model, ESC are cultured in suspension in an extracellular matrix (Matrigel) that mimics the *in vivo* basal membrane, allowing 3D cell cultures (Figure 3). In this environment, single ESC develop to form polarized spheroids or rosettes with a central lumen formed by negatively charged sialomucins, including podocalyxin (PDX), that repulse the apical cell membranes (Bedzhov and Zernicka-Goetz, 2014). This model faithfully mimics the *in vivo* process undergoing in the ICM of the blastocyst.

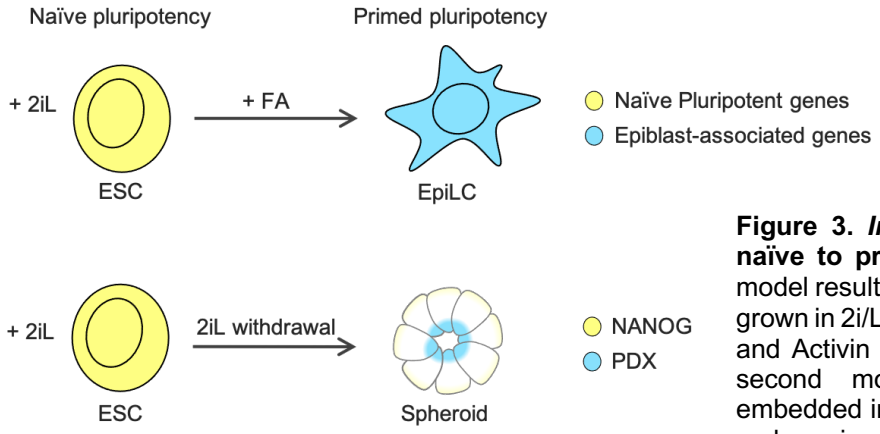


**Figure 3. *In vitro* models to mimic naïve to primed transition.** The first model results from the induction of ESC grown in 2i/LIF (2iL) to EpiLC with FGF2 and Activin A (FA) (upper panel). The second model results from ESC embedded in Matrigel that develop into embryonic rosettes (lower panel).

Since these *in vitro* models were established, multiple research groups have studied different signaling pathways and identified key molecular players and epigenetic events that participate in the naïve to primed transition (Buecker et al., 2014, Fan et al., 2020, Neagu et al., 2020). Among all these, we will focus on the genome-wide enhancer landscape reorganization observed during the transition from naïve to primed pluripotency (Buecker et al., 2014). Indeed,

analysis of the binding profile of pluripotent transcription factors, including OCT4 and OTX2, in ESC and EpiLC revealed an extensive remodeling in their binding landscape (Buecker et al., 2014). OCT4 shifts from enhancers associated with key players in naïve pluripotency and engages in new enhancer elements at genes implicated in post-implantation development (Figure 4). In addition, genes expressed in both states of pluripotency, including OCT4 itself, are characterized by a process known as differential enhancer usage where different enhancers acting on the same gene could be activated or inactivated while maintaining similar levels of gene expression during this transition. Global reorganization of the OCT4 genomic binding during naïve to primed transition is driven by increased expression of OTX2 (Buecker et al., 2014). In fact, ectopic OTX2 expression in ESC grown in naïve conditions revealed its behavior as pioneering factor engaging in previously inaccessible enhancer sites, relocating OCT4 to these sites, and inducing the expression of primed-associated genes (Buecker et al., 2014). Furthermore, enhancer decommission associated to the naïve regulatory sequences mediated by the relocation of OCT4 is followed by changes in enhancer chromatin patterns including decreased levels of H3K27ac and thus, gene silencing (Heurtier et al., 2019).

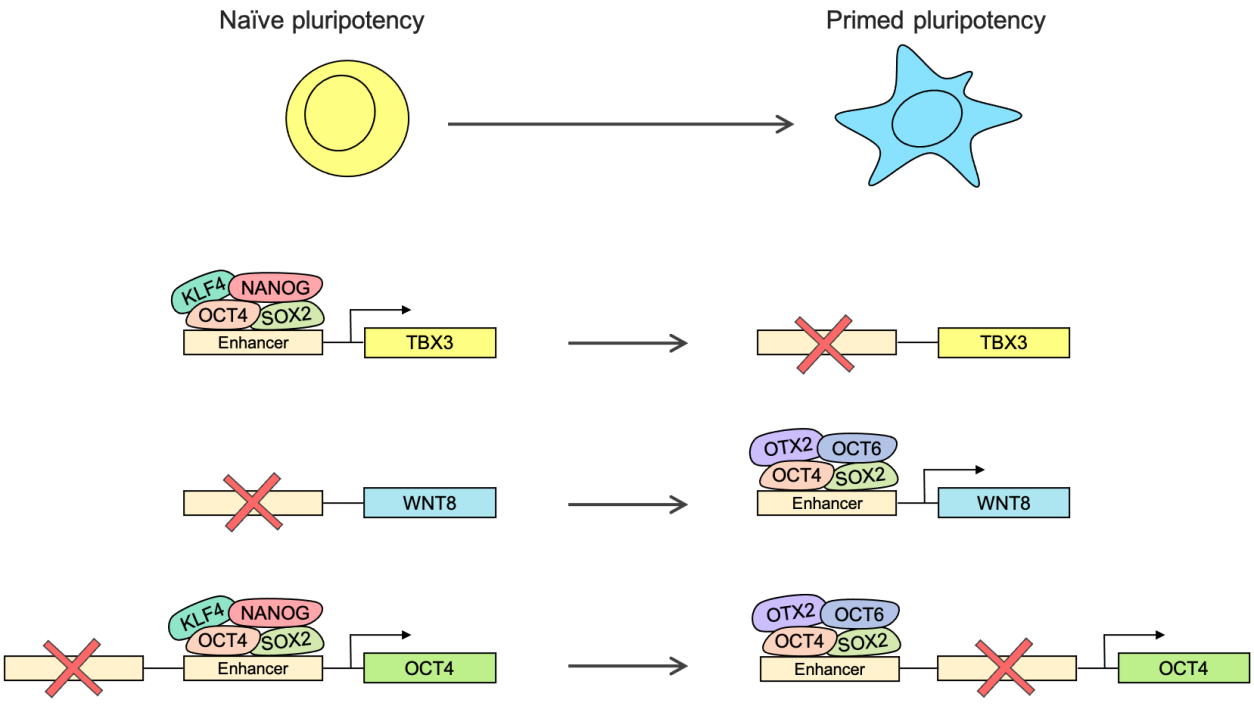


**Figure 4. Global reorganization of OCT4 binding landscape during naïve to primed transition.** OCT4 shifts from enhancers associated with naïve pluripotent genes to new enhancers at epiblast-associated genes. In addition, enhancers acting on the same gene can be activated or inactivated while maintaining similar levels of gene expression during naïve to primed transition. TBX3: Naïve-associated gene; WNT8: Primed-associated gene. OCT4: Common gene.

## Alternative states of pluripotency

As mentioned above, pluripotency should be considered as a dynamic property associated to different stem cell states and supported by a defined pluripotent transcriptional network. It is known that WNT and MEK signals mediate the transition from naïve to primed pluripotency *in vitro* and *in vivo*. While ESC depend on activated WNT signaling and the inhibition of RAS/MAPK pathway for self-renewal and the maintenance of naïve pluripotency (culture conditions with 2i), EpiSC require activation of RAS/MAPK and TGF-β signaling (culture conditions with FGF and Activin A) (Table 1) (Ying et al., 2008). For the past few years, researchers have hypothesized that an intermediate state of pluripotency, or formative period, is necessary to accomplish the extensive molecular reconfiguration of the unbiased cells within the naïve pluripotent epiblast to a primed state of pluripotency, where cells are committed for lineage specification. This hypothesis was based on the inability of ESC and EpiSC to specify the germ line. To become responsive, ESC must be differentiated to the transient population of EpiLC, suggesting that the ability for germline induction *in vivo* is a feature acquired during the developmental progression prior to EpiSC specification (Kalkan and Smith, 2014, Smith, 2017, Kinoshita and Smith, 2018). The confirmation of this hypothesis came from different groups which were able to establish stable cultures of ESC residing in an intermediate state between naïve and primed pluripotency (Neagu et al., 2020, Kinoshita et al., 2020, Yu et al., 2020, Wang et al., 2021). One of these intermediate states of pluripotency, referred as the rosette pluripotent state, was characterized by the co-expression of naïve pluripotent factors together with the transcription factor OTX2 (Neagu et al., 2020). Interestingly, it was shown that inhibition of WNT signaling mediated the transition from naïve to rosette pluripotency by inducing the expression of OTX2. Further activation of the RAS/MAPK signaling in rosette pluripotent cells promoted the progression to primed pluripotency (Neagu et al., 2020). This first work demonstrated how a discrete intermediate state of pluripotency could be stabilized *in vitro* by using specific culture conditions.

Additional groups have also recently reported the capture *in vitro* of additional states of intermediate pluripotency. These pluripotent states rely on exogenous (chimera pluripotent stem cells, XPSC; and formative pluripotent stem cells, fPSC) or autocrine (formative stem cells, FSC) FGF signaling for their self-renewal in contrast to the requirements for rosette embryonic stem cells (RSC) (Kinoshita et al., 2020, Yu et al., 2020, Wang et al., 2021). These intermediate states are characterized by their germ cell specification capacity and resemble the mouse post-

implantation epiblast between E5.5-E6.0. In addition, high levels of OTX2 have also been associated to these intermediate states of pluripotency. OTX2 expression, independent of MEK signals and efficiently repressed by the WNT pathway, is indispensable for sustaining formative pluripotency (Neagu et al., 2020, Kinoshita et al., 2020, Yu et al., 2020, Wang et al., 2021). Nevertheless, the molecular regulators involved in the maintenance of these new intermediate states of pluripotency remain unknown and a better understanding is further warranted.

**Table 1.** Features of the different mouse pluripotent stem cells.

| Feature | ESC | RSC | FSC | XPSC | fPSC | EpiSC |
|---|---|---|---|---|---|---|
| **Pluripotency** | Naïve | Intermediate | Intermediate | Intermediate | Intermediate | Primed |
| **Embryonic stage** | E3.5-E4.25 | E5.0 | E5.5-E6.0 | E5.0-E6.0 | E6.0-E6.5 | E6.5-E7.5 |
| **Culture conditions** | 2i, LIF | LIF, MEKi, WNTi | Act A, WNTi, RARi | FGF, Act A, GSK3i | Act A, WNTi | FGF, Act A |
| **Transcription Factors Expression Level** | NANOG ↑↑↑<br>KLF4 ↑↑↑<br>OTX2 ↓<br>OCT6 ↓<br>DNMT3B ↓ | NANOG ↑<br>KLF4 ↑<br>OTX2 ↑↑↑<br>OCT6 ↓<br>DNMT3B ↓ | NANOG ↓<br>KLF4 ↓<br>OTX2 ↑<br>OCT6 ↓<br>DNMT3B ↓ | NANOG ↓<br>KLF4 ↓<br>OTX2 ↑<br>OCT6 ↓<br>DNMT3B ↓ | NANOG ↓<br>KLF4 ↓<br>OTX2 ↑↑<br>OCT6 ↑↑<br>DNMT3B ↑ | NANOG ↓<br>KLF4 ↓<br>OTX2 ↑↑<br>OCT6 ↑↑↑<br>DNMT3B ↑↑ |
| **DNA methylation level** | Low | Medium | No data | No data | High | High |
| **Active pathways** | WNT | TGF- β (?) | TGF- β | FGF, TGF- β, WNT | TGF- β, FGF | FGF, TGF- β |

ESC: embryonic stem cells, RSC: rosette-like stem cells, FSC: formative stem cells, XPSC: chimera pluripotent stem cells, fPSC: formative pluripotent stem cells, EpiSC: epiblast stem cells.

## FGF and RAS/MAPK signaling during pre-implantation development

Exit from naïve pluripotency during implantation is essential to fate the epiblast cells residing in the ICM to inductive signals prior to gastrulation (Smith, 2017). Activation of the RAS/MAPK pathway by FGF4 is the key signal within the ICM of the blastocyst to fuel the exit from naïve pluripotency, promote uterus implantation and initiate a coordinated developmental

program that will establish a multi-lineage decision commitment after implantation (Bessonnard et al., 2014, Yamanaka et al., 2010, Kang et al., 2013). The cells within the ICM respond to FGF4 through FGFRI and II to stabilize the fate of PrE cells and through FGFRI to promote the maturation of pluripotent EPI cells (Kang et al., 2017). ESC depend on the FGF/MAPK signaling to transition toward EpiLC and thus, mouse embryos as well as ESC deficient for FGF4 or its receptors are unable to differentiate and progress to a later post-implantation state remaining trapped in naïve pluripotency. In addition, mouse embryos treated with MEKi showed the same phenotype (Kang et al., 2017, Kang et al., 2013, Nichols et al., 2009, Kunath et al., 2007). Despite the relevance of this pluripotent transition, the molecular mechanism and downstream effectors by which RAS/MAPK activity instructs the exit from the naïve pluripotency remain largely unknown.

## RAS proteins

RAS proteins (H-RAS, N-RAS and K-RAS) are small GTPases that are essential regulators of proliferation, differentiation and survival in eukaryotic cells (Cox and Der, 2010, Pylayeva-Gupta et al., 2011). These proteins cycle between an active (GTP-bound) and inactive (GDP-bound) state regulated by GEF (guanine exchange factors), which promote the GDP/GTP exchange, and GAP (GTPase activating proteins) that accelerate GTP hydrolysis. RAS signaling initiates at the membrane, where it integrates cues coming from a wide range of mitogens such as EGF (epidermal growth factor) or FGF through their receptors. Upon activation, RAS proteins elicit their function by triggering phosphorylation-dependent downstream signaling cascades from which the RAF/MEK/ERK (MAPK pathway) and PI3K/AKT/mTOR routes are the most studied (Figure 5). Ultimately, RAS signal is executed by transcription factors of different families including those from the FOS, JUN, MYC and the E26 transformation specific (ETS) families.

As mentioned above, in the context of the embryo development, binding of FGF4 to its receptors elicits the activation of the RAS/MAPK pathway to promote exit from naïve pluripotency. A consecutive cascade of phosphorylation and activation events in the kinases of the MAPK pathway leads to the activation of the kinase ERK which phosphorylates a wide range of nuclear and cytoplasmic proteins (Caunt et al., 2015). Among the different substrates of ERK, we will focus, due to its relevance for this Thesis work, on the ETS family of transcription factors.

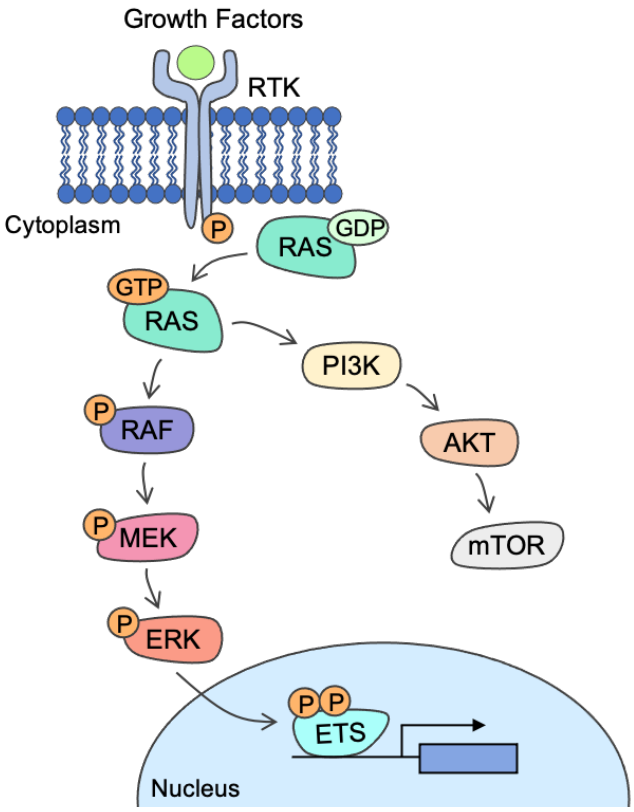


**Figure 5. Main RAS effector pathways.** Schematic representation of the MAPK pathway and the PI3K/AKT/mTOR pathway.

## The ETS family

The ETS family is one of the largest families of transcriptional regulators characterized by a conserved DNA binding domain (ETS domain) which binds DNA sequences centered over a GGAA/T core motif (Sharrocks, 2001). The first ETS-domain containing gene described, v-ets, was cloned from the avian erythroblastosis virus E26 (Leprince et al., 1983). Since then, 27 genes in mouse (28, in human) have been identified in this large family of transcription factors that is specific to metazoan (Sizemore et al., 2017). The ETS factors are involved in the regulation of a wide variety of functions including cellular proliferation, differentiation, apoptosis and transformation (Findlay et al., 2013).

The role of the ETS family during embryonic development has not been studied in depth. The expression level of several ETS factors, such as SPIC, ETSRP71 or ELF3, increases after fertilization and remains at a high level until the blastocyst stage. For instance, the expression of SPIC increases at the 2-cell stage and then decreases at the blastocyst stage. Interestingly,

downregulation of SPIC as well as the two ETS factors ETSRP71 and ELF3, reduced the expression levels of eIF-1A and OCT4 (Kageyama et al., 2006). Furthermore, it has been shown that ETS members of the PEA3 group, including ETV1, ETV4 and ETV5, are also involved in early embryonic development (de Launoit et al., 2006, Lu et al., 2009). ETV4 and ETV5, although functionally redundant, are expressed in ESC and are involved in cell proliferation and induction of differentiation-associated genes. Indeed, deletion of both, ETV4 and ETV5, compromises proliferation and differentiation of ESC (Akagi et al., 2015). Recently, a different study showed that elimination of ETV5 together with two transcriptional repressors (TCF3 and RBPJ) effectively prohibits ESC progression to primed pluripotency (Kalkan et al., 2019). Combined, these results suggest that the family of ETS transcription factors play important roles during pre-implantation development.

## ERF

While ETS transcription factors are best known as transcriptional activators, there are also examples within this family of transcriptional repressors, such as ERF. ERF is a transcription factor that shuffles between the nucleus and cytoplasm in a phosphorylation-dependent manner (Sgouras et al., 1995). In the absence of RAS/MAPK signaling, ERF remains unphosphorylated in the nucleus. Upon growth factor stimulation, ERF is phosphorylated by ERK in multiple residues, translocated out of the nucleus and kept inactive in the cytoplasm (Sgouras et al., 1995, Le Gallic et al., 1999, Le Gallic et al., 2004). ERF has been associated to the control of proliferation and differentiation. Indeed, over-expression of ERF induces cell cycle arrest and impairs RAS-driven cell transformation by its ability to potently repress the transcription of c-Myc (Verykokakis et al., 2007, Le Gallic et al., 1999). During embryonic development, ERF is required for chorionic trophoblast differentiation and homozygous deletion of ERF in mice leads to embryo death by E10.5 (Papadaki et al., 2007, Vorgia et al., 2017). Interestingly, ERF was also identified as a regulator of osteogenic stimulation since reduced dosage of ERF causes a premature fusion of the cranial sutures, or craniosynostosis, in humans and mice (Twigg et al., 2013).

Activation of the RAS/MAPK pathway is the trigger to exit naïve pluripotency in ESC. However, how this signaling facilitates the transition to primed pluripotency remains unknown. In the last few years, we have focused our studies in understanding this process. For this, we have used an inducible ESC genetic model in which we can deplete of all RAS proteins (N-, H- and K-

RAS) (Drosten et al., 2010), allowing us to specifically dissect the role of the downstream RAS/MAPK regulators.

This genetic model consists of an ESC line (N-RAS$^{-/-}$; H-RAS$^{-/-}$; K-RAS$^{lox/lox}$; Ubiq-Cre$^{ERT2}$, or RAS$^{lox/lox}$) deficient for N- and H-RAS while the remaining K-RAS can be eliminated upon addition of 4-hydroxytamoxifen (OHT) (Mayor-Ruiz et al., 2018, Drosten et al., 2010). In our previous work, we showed that RAS nullyzygosity (RAS$^{KO}$ hereafter) reduces the growth of ESC and prohibits their differentiation. Importantly, we identified ERF as a key mediator of RAS/MAPK pathway (Mayor-Ruiz et al., 2018). We demonstrated that ERF, in the absence of MAPK signaling, is prominently nuclear and binds to ESC-specific enhancer regulatory sequences affecting key pluripotent and developmental genes (Mayor-Ruiz et al., 2018). We also observed that loss of ERF rescued the proliferative defects of RAS$^{KO}$ ESC and restored their capacity to differentiate *in vitro* as well as *in vivo* (Mayor-Ruiz et al., 2018). Nevertheless, although we identified ERF as a critical factor for licensing RAS$^{KO}$ ESC to differentiate, its precise temporal requirement or the molecular mechanism underlying our observations were unknown. Therefore, identifying how the transcription factor ERF, a key mediator of the response to RAS activation in ESC, integrates FGF activation and coordinates the naïve-to-primed transition in ESC is the main goal of this Thesis work.

# OBJECTIVES

1. To characterize the phenotype of RAS-deficient cells during the transition from naïve to primed pluripotency.

2. To analyze the role of ERF during early embryonic development.

3. To identify the molecular mechanisms by which ERF regulates the transition from naïve to primed pluripotency.

# MATERIALS AND METHODS

## Isolation, immunostaining and imaging of mouse embryos

C57BL/6J mice were obtained from the Jackson Laboratory in compliance with the NIH Animal Care & Use Committee (ACUC) Guideline for Breeding and Weaning. Mouse embryos were collected in M2 media (Sigma-Aldrich) at indicated time points from 4 weeks old female mice injected intraperitoneally with 5 IU Pregnant Mare Serum Gonadotropin (PMSG, Prospec) followed by 5 IU human Chorionic Gonadotropin (hCG, Sigma-Aldrich) 46-48 hours later and/or from eight weeks old naturally pregnant females. Embryos were fixed in 4% Paraformaldehyde (Electron Microscopy Sciences) for 10 minutes, permeabilized for 30 minutes in 0.3% Triton X-100 and 0.1 M Glycine in PBS 1X and blocked for 1 hour (1% BSA, 0.1% Tween in PBS 1X). Embryos were incubated overnight with primary antibodies and following day with secondary antibodies for 1 hour at room temperature. Embryos were imaged using a Nikon Ti2-E microscope (Nikon Instruments) equipped with a CSU-W1 spinning disk (Yokogawa), Photometrics Prime BSI sCMOS (Photometrics), and 60x Nikon Apochromat TIRF objective (NA = 1.49). Z-stacks were acquired with a x-y pixel size of 0.11 mm and z-step of 0.9 mm. For quantification, embryo z-stack images were quantified using Imaris Bitplane (Oxford Instruments). 3D surfaces were rendered based on nuclear DAPI-staining and the corresponding regions were used to quantify the fluorescence intensity of ERF, NANOG and KLF4. The following embryos and cells were used for quantification (Figure 6A, E): Exp 1: E2.75: 3 Embryos, 24 cells in total. E3.5: 3 Embryos, 459 cells total, E4.0: 4 Embryos, 168 cells total, E4.75: 1 Embryo: 75 cells. Exp 2: E3.5: 8 embryos, E3.75: 4 embryos, E4.0: 6 embryos. See Table 2 for antibody information.

## Cell culture

N-RAS$^{-/-}$; H-RAS$^{-/-}$; K-RAS$^{lox/lox}$; Ubiq-Cre$^{ERT2}$ (RAS$^{lox/lox}$) (Drosten et al., 2010) ESC were grown in N2B27 media supplemented with 2iL (1 mM PD0325901, 3 mM CHIR99021, both from Tocris and 1:500 LIF, made in house). N2B27 media consisted of a 1:1 mix of DMEM/F12 and Neurobasal Medium, 1X N2 supplement, 1X B27 supplement, 0.1 mM nonessential amino acids, 55 µM β-mercaptoethanol and 1% penicillin/streptomycin (all from Life Technologies). Cells were routinely cultured in 0.1% gelatinized plates and passaged with Accutase (Gibco) unless otherwise indicated. To induce CRE-mediated deletion of the remaining K-RAS alleles, we incubated RAS$^{lox/lox}$ ESC with 1 µM 4-hydroxytamoxifen (OHT, Sigma-Aldrich) for 6 days before

performing any experiment. HEK293T (American Type Culture Collection) cells were grown in DMEM, 10% FBS, and 1% penicillin/streptomycin.

## Differentiation to EpiLC

To induce EpiLC differentiation, ESC were grown for few passages in plates preincubated with 10 µg/ml polyL-ornithine and 5 µg/ml laminin (Corning). A total of 200,000–300,000 cells per 10 $cm^2$ were plated on plates pretreated with 5 µg/ml Fibronectin (Millipore) in N2B27 media supplemented with 1% KOSR, 12 ng/ml FGF2 (R&D systems) and 20 ng/ml Activin A (PeproTech) for 48 hours including daily media changes. To maintain EpiLC in culture, ESC were plated in N2B27 media with 12 ng/ml FGF2, 20 ng/ml Activin A and 1 mM XAV939 on Fibronectin-coated plates at a density of 10,000 cells per $cm^2$. Media was changed every other day and passaged every 2-3 days.

## Generation of REX1-deGFP reporter ESC

To target a short half-life form of eGFP (deGFP) in the endogenous REX1 gene, we generated a targeting vector by inserting deGFP in pCR®-Blunt II TOPO® (Zero Blunt TOPO PCR cloning kit, Invitrogen). Homology arms from endogenous sequences upstream of the start codon and downstream of the stop codon from REX1 were PCR-amplified and cloned to flank pCR®-Blunt II TOPO®-deGFP. In addition, specific small guide RNA (sgRNA) sequences targeting the surroundings of the REX1 start codon were cloned into the plasmid pX330-U6-Chimeric_BB-CBh-hSpCas9 (Gift from Feng Zhang, Addgene, 42230) (Cong et al., 2013). The sequences of the sgRNAs were designed with the Genetic Perturbation Platform sgRNA designer tool (https://portals.broadinstitute.org/gpp/public/analysis-tools/sgrna-design). Both plasmids were transfected in ESC using Jetprime (Polyplus transfection) to generate the targeting and cells were sorted based on GFP intensity to isolate individual clonal ESC lines. See Table 3 for primer information.

## Generation of DOX-inducible DNMT3B ESC

To generate ESC lines carrying a DOX-inducible DNMT3B-PiggyBac construct, the coding sequence for DNMT3B was amplified from cDNA and subcloned into the plasmid PB-TRE-dCas9-

VPR (Gift from George Church, 63800, Addgene), after removing the dCas9-VPR insert. DOX-inducible PiggyBac-DNMT3B plasmid together with a plasmid encoding for a supertransposase were co-transfected in ESC and selected with Hygromycin (200 µg/ml) for one week. See Table 3 for primer information.

## Clonogenicity Assay

ESC were withdrawn of 2iL for 48 hours and plated at single cell density (50 cells/$cm^2$) in N2B27 media with 2iL on plates coated with 0.1% gelatin (Sigma). At day 5, alkaline phosphatase staining was performed using the Alkaline Phosphatase Detection Kit (Millipore). Colonies were counted manually. At least three independent experiments with three replicates per experiment were performed.

## Reporter Assay to determine enhancer activity

Reporter constructs were generated by amplifying the three ERF-bound enhancer regions within the PRDM14 super-enhancer by PCR (see Figure 20B to visualize the enhancers). PCR fragments were cloned in a vector upstream of a GFP sequence containing only a minimal promoter sequence and verified by sequencing. To perform the assay, each individual reporter plasmid containing the PRDM14 enhancer was co-transfected with a plasmid expressing constitutively the mCherry protein (pINTO_mCherry) in $RAS^{lox/lox}$ and $ERF^{KO}$ ESC. Three days after transfection, ESC were collected and run by flow cytometry to detect GFP and mCherry expression. Mean intensity for each fluorescent protein was calculated for every condition in GFP and mCherry positive ESC. Then, GFP mean intensity was normalized using the mCherry mean intensity. At least two experiments were performed in two independent ESC clones per genotype. See Table 3 for primer information.

## Generation and immunostaining of self-organizing ESC spheres

ESC growing on gelatinized plates in N2B27 media with 2iL were dissociated with Accutase and washed with PBS before their resuspension in growth factor reduced Matrigel (Corning) at a concentration of 10,000 cells per 20 µl of Matrigel. The suspension was deposited in drops in 8-µwell Ibidi microplates and incubated at 37°C until the Matrigel solidified. Wells were

then filled with N2B27 media without 2iL and cultured for 48-72 hours at 37°C and 5% CO2. To inhibit WNT signaling, embryonic spheres were incubated with 2 µM IWR-1 for the duration of the assay. ESC-derived spheres were fixed in 4% Paraformaldehyde for 10 minutes at room temperature. Permeabilization was performed in PBS containing 0.3% Triton X-100 (Sigma) and 0.1 M glycine (Sigma) for 30 minutes at room temperature. Spheres were incubated with primary antibodies at 4°C overnight, followed by incubation with corresponding fluorescently conjugated Alexa Fluor secondary antibodies for 2 hours at room temperature. Both primary and secondary antibodies were diluted in PBS containing 1% BSA (Sigma) and 0.1% Tween20 (Sigma). See Table 2 for antibody information.

## Western blot

Cells were lysed in 50 mM Tris pH 8, 8 M Urea (Sigma) and 1% Chaps (Millipore) followed by 30 minutes of shaking at 4°C. 20 µg of supernatants were run on 4%-12% NuPage Bis-Tris Gel (Invitrogen) and transferred onto Nitrocellulose Blotting Membrane (GE Healthcare). Membranes were blocked in 5% skim milk (Millipore) and 0.1% Tween 20 (Sigma) in PBS. Membranes were incubated with the primary antibody overnight at 4°C, followed by incubation with HRP-conjugated secondary antibodies for 1 hour at room temperature. Membranes were developed using SuperSignal West Pico PLUS (Thermo Scientific). See Table 2 for antibody information.

## Dot blot

Trypsinized ESC were lysed for 2-3 hours at 55°C with lysis buffer (100 mM Tris-HCl pH 8, 5 mM EDTA, 0.2% SDS, 20 mM NaCl and 100 µg/ml Proteinase K). DNA was isolated by adding an equal volume of Phenol/Chloroform/Isoamyl to the samples and using phase-lock tubes (5PRIME Phase Lock GelTM Heavy, Quantabio), followed by an extraction with identical volume of Chloroform. DNA was precipitated with 2 volumes of 100% Ethanol plus 0.3 M sodium acetate, washed with 70% Ethanol and resuspended in water. A total of 500 ng of DNA was diluted in 0.3 M NaOH and denatured at 42°C for 12 minutes. After incubation, the samples were rapidly transferred by spotting each sample into a nitrocellulose membrane (Nitrocellulose Blotting Membrane, GE Healthcare). After the transfer, DNA was crosslinked with a Stratalinker® UV crosslinker (Stratagene) using the Autocrosslink setting. The membrane was blocked in 5% skim milk (Millipore) and 0.1% Tween 20 (Sigma) in PBS, incubated with anti-5mC antibody overnight

at 4°C, followed by incubation with HRP-conjugated secondary antibody for 1 hour at room temperature. Membrane was developed using SuperSignal West Pico PLUS (Thermo Scientific). See Table 2 for antibody information.

## Flow cytometry

For flow cytometry experiments, cells were dissociated into single cell suspensions and analyzed for GFP gene expression using a FACS Fortessa (BD Biosciences). DAPI was added to detect cells with compromised membrane integrity. Data was analyzed using FlowJo. At least two independent experiments were performed.

## Immunofluorescence

Cells were fixed in 4% Paraformaldehyde (Electron Microscopy Sciences) for 10 minutes at room temperature, permeabilized in 100 mM Tris-HCl pH 7.4, 50 mM EDTA pH 8.0, 0.5% Triton X-100 and incubated with the corresponding primary antibodies overnight. This was followed by incubation with corresponding fluorescently conjugated Alexa Fluor secondary antibodies for 2 hours at room temperature. Both primary and secondary antibodies were diluted in PBS containing 1% BSA (Sigma) and 0.1% Tween20 (Sigma). Images were acquired using either a Nikon spinning disk confocal microscope (CSU-W1) or a Zeiss LSM880 Airyscan microscope. See Table 2 for antibody information.

## High throughput imaging (HTI)

A total of 10,000-20,000 ESC were plated in 2iL conditions on gelatin or 5 µg/ml Fibronectin (Millipore) in µCLEAR bottom 96-well plates (Greiner Bio-One, 655087). ESC were either maintained in 2iL conditions or treated with FA for the indicated times. Staining was performed using standard procedures. DNA was stained using DAPI.

Images were automatically acquired using a CellVoyager CV7000 high throughput spinning disk confocal microscope (Yokogawa, Japan). Each condition was performed in triplicate wells and/or at least 9 different fields of view (FOV) were acquired per well. High-Content Image (HCI) analysis was performed using the Columbus software (PerkinElmer). In brief, nuclei were first segmented using the DAPI channel. Mean fluorescence intensities for OTX2, ERF, ESRRB

or NANOG signal were calculated over the nuclear masks in their respective channels. Single cell data obtained from the Columbus software was exported as flat tabular .txt files, and then analyzed using RStudio version 1.2.5001, and plotted using Graphpad Prism version 9.0.0.

## RNA-seq

RNA was isolated using the ISOLATE II RNA Mini Kit (Bioline) following manufacturer's recommendations. DNA libraries for RNA-seq analysis were prepared using NEBNext Ultra II Directional RNA Library Prep Kit for Illumina (New England Biolabs, NEB) and NEBNext rRNA Depletion Kit (Human/Mouse/Rat) (NEB) according to the manufacturer's protocol. Sequencing was performed on the Illumina NextSeq550 (75bp pair-end reads).

## CUT&RUN

The CUT&RUN protocol was slightly modified from (Skene and Henikoff, 2017, Meers et al., 2019). In brief, cells were washed thrice with Wash Buffer (20 mM HEPES-KOH pH 7.5, 150 mM NaCl, 0.5 mM spermidine, Roche complete Protease Inhibitor tablet EDTA free) and bound to activated Concanavalin A beads (Polysciences) for 10 minutes at room temperature. Cells were then permeabilized in Digitonin Buffer (0.05 % Digitonin and 0.1% BSA in Wash Buffer) and incubated with corresponding antibodies at 4°C for 2 hours. For negative controls, Guinea Pig anti-Rabbit IgG (Antibodies-online) was used. Following antibody incubation, cells were washed with Digitonin Buffer and incubated with a hybrid protein A-protein G-Micrococcal nuclease (pAG-MNase) at 4°C for 1 hour. Samples were washed in Digitonin Buffer, resuspended in 150 µl Digitonin Buffer and equilibrated to 0°C on ice water for 5 minutes. To initiate MNase cleavage, 3 µl 100 mM $CaCl_2$ was added to cells and after 1 hour of digestion, reactions were stopped with the addition of 150 µl 2x Stop Buffer (340 mM NaCl, 20 mM EDTA, 4 mM EGTA, 0.02 % Digitonin, 50 µg/ml RNase A, 50 µg/ml Glycogen). Samples were incubated at 37°C for 10 minutes to release DNA fragments and centrifuged at 16,000 g for 5 minutes. Supernatants were collected and a mix of 1.5 µl 20% SDS and 2.25 µl 20 mg/ml Proteinase K was added to each sample and incubated at 65°C for 35 minutes. DNA was precipitated with ethanol and sodium acetate and pelleted by high-speed centrifugation at 4°C, washed, air-dried and resuspended in 10 µ 0.1x TE. See Table 2 for antibody information.

## CUT&RUN library preparation and sequencing

The entire precipitated DNA obtained from CUT&RUN was used to prepare Illumina compatible sequencing libraries. In brief, end-repair was performed in 50 µl of T4 ligase reaction buffer, 0.4 mM dNTPs, 3 U T4 DNA polymerase (NEB), 9 U T4 Polynucleotide Kinase (NEB) and 1 U Klenow fragment (NEB) at 20°C for 30 minutes. End-repair reaction was cleaned using AMPure XP beads (Beckman Coulter) and eluted in 16.5 µl of Elution Buffer (10 mM Tris-HCl pH 8.5) followed by A-tailing reaction in 20 µl of dA-Tailing reaction buffer (NEB) with 2.5 U of Klenow fragment exo- (NEB) at 37°C for 30 minutes. The 20 µl of the A-tailing reaction were mixed with Quick Ligase buffer 2X (NEB), 3000 U of Quick Ligase (NEB) and 10 nM of annealed adaptor (Illumina truncated adaptor) in a volume of 50 µl and incubated at room temperature for 20 minutes. The adaptor was prepared by annealing the following HPLC-purified oligos: 5'-Phos/GATCGGAAGAGCACACGTCT-3' and 5'-ACACTCTTTCCCTACACGACGCTCTTCCGATC∗T-3' (∗phosphorothioate bond). Ligation was stopped by adding 50 mM of EDTA, cleaned with AMPure XP beads and eluted in 14 µl of Elution Buffer. All volume was used for PCR amplification in a 50 µl reaction with 1 µM primers TruSeq barcoded primer p7 5'-CAAGCAGAAGACGGCATACGAGATXXXXXXXXGTGACTGGAGTTCAGACGTGTGCTCTTCCGATC∗T-3' and TruSeq barcoded primer p5 5'-AATGATACGGCGACCACCGAGATCTACACXXXXXXXXACACTCTTTCCCTACACGACGCTCTTCCGATC*T-3' (∗ represents a phosphothiorate bond and XXXXXXXX a barcode index sequence), and 2X Kapa HiFi HotStart Ready mix (Kapa Biosciences). The temperature settings during the PCR amplification were 45 seconds at 98°C followed by 15 cycles of 15 seconds at 98°C, 30 seconds at 63°C, 30 seconds at 72°C and a final 5-minute extension at 72°C. PCR reactions were cleaned with AMPure XP beads (Beckman Coulter), run on a 2% agarose gel and a band of 300bp approximately was cut and gel purified using QIAquick Gel Extraction Kit (QIAGEN). Library concentration was determined with KAPA Library Quantification Kit for Illumina Platforms (Kapa Biosystems). Sequencing was performed on the Illumina NextSeq550 (75bp pair-end reads).

## RRBS

DNA libraries for RRBS analysis were prepared using the Premium RRBS kit (Diagenode) following manufacturer’s recommendations. Sequencing was performed on the Illumina NextSeq550 (75bp single-end reads).

## Sequencing data analysis

The following sequencing data processing were performed with the help of Desiree Tillo (Genetics Branch, CCR, NCI, NIH). In addition, further analyses with processed data were performed using the platform DNAnexus (https://www.dnanexus.com/).

*RNA-seq:*

RNA-seq reads were adapter trimmed using fastp v.0.20.0 (Chen et al., 2018). Transcript expression was quantified via mapping to mouse gencode v25 transcripts using salmon (Patro et al., 2017). Identification of differentially expressed genes between samples was performed using DESEQ2 (PMID: 25516281). RNA-seq coverage tracks were generated by aligning RNA-seq reads to UCSC version mm10 of the mouse genome using the STAR v2.6.1a aligner (Dobin et al., 2013) followed by application of the 'bamCoverage' utility from deeptools (Ramirez et al., 2016) to generate signal track files with the following parameters: normalization=RPKM, bin_size=50, smooth_length=1. For comparison to other published RNA-seq data sets, gene counts across samples were quantile-normalized using the limma package (Ritchie et al., 2015). Batch correction was then performed on quantile-normalized counts using COMBAT (Johnson et al., 2007). See Table 4 for further software and algorithm information.

*CUT&RUN:*

Data were processed using a modified version of Cut&RunTools (Zhu et al., 2019). Reads were adapter trimmed using fastp v.0.20.0 (Chen et al., 2018). An additional trimming step was performed to remove up to 6bp adapter from each read. Next, reads were aligned to the mm10 genome using bowtie2 (Langmead and Salzberg, 2012) with the 'dovetail' and 'sensitive' settings enabled. Normalized (RPKM) signal tracks were generated using the 'bamCoverage' utility from deepTools with parameters bin-size=25, smooth length=75, and 'center_reads' and 'extend_reads' options enabled (Ramirez et al., 2016). See Table 4 for further software and algorithm information.

*Processing for published ChIP-seq datasets:*

External next generation sequencing data were downloaded from the Sequence Read Archive (SRA) and analyzed as follows. These analyses include a re-analysis of our original datasets (Mayor-Ruiz et al., 2018). Reads were aligned to the mm10 genome using bowtie2 (Langmead and Salzberg, 2012). Duplicate reads were removed using MarkDuplicates from the

Picard toolkit (http://broadinstitute.github.io/picard/). Normalized (RPKM) signal tracks were generated bamCoverage utility from deepTools (Ramirez et al., 2016), using the parameters bin-size=25, smooth length=75, 'center_reads' and 'extend_reads'. For paired-end data, read mates were extended to the fragment size defined by the two read mates. For single-end ChIP-seq data, reads were extended to the estimated fragment length estimated by phantompeakqualtools (Kharchenko et al., 2008). See Table 4 for further software and algorithm information.

*Identification of OCT4 binding sites in ESC and EpiLC:*

Fastq files from published OCT4 ChIP-seq data for ESC (SRR1202455, SRR1202456), EpiLC plus and minus Activin A (SRR1202468, SRR1202469), and associated input controls (SRR1202465, SRR1202464, SRR1202477 SRR1202478) (Buecker et al., 2014) were downloaded from the Sequence Read Archive (SRA). Single-end reads were aligned to the mm10 genome using bwa (Li and Durbin, 2009). Duplicate reads were removed using MarkDuplicates from the Picard toolkit (http://broadinstitute.github.io/picard/), and peaks for each sample were called using macs2 (Zhang et al., 2008) with q-value cutoff <0.01 and extension length determined using phantompeakqualtools (Kharchenko et al., 2008). Diffbind using the DeSeq2 method was used to determine differentially bound peaks, treating EpiLC plus and minus Activin A samples as replicate experiments as was done in the original study (Buecker et al., 2014). Peaks were determined to be ESC- or EpiLC-specific if they differed by 2-fold read concentration with p-val<0.01 and FDR <0.03. A subset of peaks with > mean read concentration for EpiLC and ESC with <0.5-fold difference was selected as "common" or shared peaks. See Table 4 for further software and algorithm information.

*RRBS:*

Single-end RRBS reads were adapter and quality trimmed (phred33 score>=20) using trimgalore v0.6.5 (http://www.bioinformatics.babraham.ac.uk/projects/trim_galore) with the RRBS option invoked. Bismark v0.22.1 (Krueger and Andrews, 2011) was used to align reads to UCSC version mm10 of the mouse genome. CpG methylation was extracted using bismark ignoring the first 4 bases of the read after inspection of m-bias plots. Methylation summary statistics were computed using the methylKit package (Akalin et al., 2012). See Table 4 for further software and algorithm information.

**Table 2.** List of antibodies used in this study.

| **ANTIBODIES** | | | |
|---|---|---|---|
| REAGENT | DILUTION | SOURCE | REFERENCE |
| ERF Antibody (E-9) | WB (1:500), IF (1:100) | Santa Cruz Biotechnology | Cat# sc-398269 |
| Anti-Nanog antibody | WB (1:500), IF (1:100) | Abcam | Cat# ab80892 |
| Anti Nanog (Mouse) pAb | CUT&RUN (1 µg) | Cosmo Bio USA | Cat# REC-RCAB002P-F |
| Mouse KLF4 Antibody | IF (1:250) | R&D systems | Cat# AF3158 |
| Mouse Podocalyxin Antibody | IF (1:500) | R&D systems | Cat# MAB1556 |
| Human Otx2 Antibody | IF (1:1000) | R&D systems | Cat# AF1979 |
| Anti-Otx1 + Otx2 antibody | CUT&RUN (1 µg) | Abcam | Cat# ab21990 |
| Alexa Fluor™ 488 Phalloidin | IF (1:1000) | Invitrogen | Cat# A12379 |
| Anti-OCT6 Antibody, clone KT110 | IF (1:100) | Millipore | Cat# MABN738 |
| Human ERR beta/NR3B2 Antibody | IF (1:100) | R&D systems | Cat# PP-H6705-00 |
| Anti-Sox2 Antibody | CUT&RUN (1 µg) | Millipore | Cat# AB5603 |
| Anti-Histone H3 (acetyl K27) antibody | CUT&RUN (1 µg) | Abcam | Cat# ab4729 |
| Anti-Sox2 (D9B8N) antibody | IF (1:100) | Cell Signaling | Cat# 23064S |
| p44/42 MAPK (Erk1/2) Antibody | WB (1:1000) | Cell Signaling | Cat# 9102 |
| Phospho-p44/42 MAPK (Erk1/2) (Thr202/Tyr204) Antibody | WB (1:1000) | Cell Signaling | Cat# 9101 |
| GATA6 Antibody | IF (1:100) | R&D systems | Cat# AF1700, |
| LIN28A (D1A1A) XP® Rabbit mAb | WB (1:1000) | Cell Signaling | Cat# 8641 |
| LIN28B Antibody | WB (1:1000) | Cell Signaling | Cat# 5422 |
| Monoclonal Anti-α-Tubulin antibody | WB (1:50,000) | Sigma-Aldrich | Cat# T9026 |
| Anti-Dnmt3b antibody | WB (1:1000) | Abcam | Cat# ab122932 |
| DNMT3A Antibody | WB (1:500) | Novus Biological | Cat# NB120-13888 |
| Pan-RAS (Ab-3) Mouse mAb (RAS 10) | WB (1:500) | Millipore | Cat# OP40-100UG |
| Anti-5-methylcytosine (5-mC) antibody [33D3] | Dot blot (1:500) | Abcam | Cat# ab10805 |
| Guinea Pig anti-Rabbit IgG (Heavy & Light Chain) Antibody | CUT&RUN (1 µg) | Antibodies-Online | Cat# ABIN101961 |
| Goat anti-Rabbit IgG (H+L) Secondary Antibody, HRP | WB (1:5000) | Thermo Fisher Scientific | Cat# 31466 |
| Goat anti-Mouse IgG (H+L) Secondary Antibody, HRP | WB (1:5000) | Thermo Fisher Scientific | Cat# 31431 |
| Chicken anti-Rabbit IgG (H+L) Cross-Adsorbed Secondary Antibody, Alexa Fluor 488 | IF (1:1000) | Thermo Fisher Scientific | Cat# A-21441 |

| | | | |
|---|---|---|---|
| Goat anti-Mouse IgG (H+L) Cross-Adsorbed Secondary Antibody, Alexa Fluor 568 | IF (1:1000) | Thermo Fisher Scientific | Cat# A-11004 |
| Donkey anti-Mouse IgG (H+L) Highly Cross-Adsorbed Secondary Antibody, Alexa Fluor 568 | IF (1:1000) | Thermo Fisher Scientific | Cat# A10037 |
| Chicken anti-Goat IgG (H+L) Cross-Adsorbed Secondary Antibody, Alexa Fluor 488 | IF (1:1000) | Thermo Fisher Scientific | Cat# A-21467 |
| Chicken anti-Rabbit IgG (H+L) Cross-Adsorbed Secondary Antibody, Alexa Fluor 647 | IF (1:1000) | Thermo Fisher Scientific | Cat# A-21443 |
| Donkey anti-Rabbit IgG (H+L) Highly Cross-Adsorbed Secondary Antibody, Alexa Fluor 568 | IF (1:1000) | Thermo Fisher Scientific | Cat# A10042 |
| Chicken anti-Rat IgG (H+L) Cross-Adsorbed Secondary Antibody, Alexa Fluor 488 | IF (1:1000) | Thermo Fisher Scientific | Cat# A-21470 |
| Chicken anti-Mouse IgG (H+L) Cross-Adsorbed Secondary Antibody, Alexa Fluor 647 | IF (1:1000) | Thermo Fisher Scientific | Cat# A-21463 |

**Table 3.** List of primers used in this study.

| **OLIGONUCLEOTIDES** | |
|---|---|
| NAME | 5’ to 3’ SEQUENCE |
| 5’-REX1-KpnI-F (Primer for left homology REX1 arm) | ACGTGGTACCTCTTTGCCTTACAGAGAAGCC |
| 5’-REX1-SacI-R (Primer for left homology REX1 arm) | ACGTGAGCTCGTTGTCTTAGCTGCTTCCTTC |
| 3’-REX1-NotI-F (Primer for right homology REX1 arm) | ACGTGCGGCCGCAGGTGGAGACAGATTGTCCTC |
| 3’-REX1-XhoI-F (Primer for right homology REX1 arm) | ACGTCTCGAGTTGCCTTAAGTTCTGTATGC |
| eGFPd2-F | ACAACATGGTGAGCAAGGGCGAGGAGC |
| eGFPd2-R | ACGTCTACACATTGATCCTAGCAGAAG |
| sgRNA-REX1-F1 | CACCGAGTGGCCAGAAAGGGCCGGG |
| sgRNA-REX1-R1 | AAACCCCGGCCCTTTCTGGCCACTC |
| sgRNA-REX1-F2 | CACCGCCATATCCGCATCCACACCG |
| sgRNA-REX1-R2 | AAACCGGTGTGGATGCGGATATGGC |
| Cloning of DNMT3B in PB-TRE-dCas9-VPR-F | GCTAGCTAGCACCATGAAGGGAGACAGCAGACATC |
| Cloning of DNMT3B in PB-TRE-dCas9-VPR-R | GCTAGTTTAAACTTCACAGGCAAAGTAGTCCTTC |

| | |
|---|---|
| Cloning of PRDM14_Enhancer_F1 | GATTCTCGAGGCTATTCAGTAGGTGTCGATGTTCTAC |
| Cloning of PRDM14_Enhancer_R1 | GATGAATTCTCAATAGACCAGGCTGGCCTTAACCC |
| Cloning of PRDM14_Enhancer_F2 | GATTCTCGAGTGAAATGTGTCCTGTAGAACCACCAG |
| Cloning of PRDM14_Enhancer_R2 | GTTTCCCCAGGAATTCTCTGTGGAC |
| Cloning of PRDM14_Enhancer_F3 | GATTCTCGAGATTCTAAGGTCTGGCTGTACCTTTTT |
| Cloning of PRDM14_Enhancer_R3 | GTAGACATAATAGCAACAGAC |

**Table 4.** List of software and algorithms used in this study.

| **SOFTWARE AND ALGORITHMS** | | |
|---|---|---|
| RESOURCE | SOURCE | WEBSITE |
| Cut&RunTools | Zhu et al., 2019 | https://bitbucket.org/qzhudfci/cutruntools/ |
| fastp v.0.20.0 | Chen et al., 2018 | https://github.com/OpenGene/fastp |
| bowtie2 | Langmead et al., 2012 | http://bowtie-bio.sourceforge.net/bowtie2/index.shtml |
| macs2 | Zhang et al., 2008 | https://github.com/macs3-project/MACS |
| deepTools | Ramirez et al., 2016 | https://github.com/deeptools/deepTools |
| Picard toolkit | | http://broadinstitute.github.io/picard/ |
| phantompeakqualtools | Kharchenko et al., 2008 | https://github.com/kundajelab/phantompeakqualtools |
| Diffbind v3.0.5 | Stark R. and Brown G. D. (2011). | https://bioconductor.org/packages/release/bioc/html/DiffBind.html |
| trimgalore v0.6.5 | | http://www.bioinformatics.babraham.ac.uk/projects/trim_galore |
| Bismark v0.22.1 | Krueger et al., 2011 | https://github.com/FelixKrueger/Bismark |
| methylKit v1.14.2 | Akalin et al., 2012 | https://bioconductor.org/packages/release/bioc/html/methylKit.html |
| Prism 8 | GraphPad | https://www.graphpad.com/ |
| FlowJo (10.1) | FlowJo LLC | https://www.flowjo.com/ |
| DNAnexus | DNAnexus | https://www.dnanexus.com/ |
| IGV | Robinson et al., 2011 | https://igv.org/ |
| R (3.5 and 4.0) | | www.r-project.org |
| GREAT | McLean et al., 2010 | http://great.stanford.edu/public/html/ |
| DESEQ2 | Love et al., 2014 | http://bioconductor.org/packages/release/bioc/html/DESeq2.html |

# RESULTS

## ERF expression is associated to naïve pluripotency

As mentioned in the introduction, we have recently identified the transcription factor ERF as an important regulator downstream of the RAS pathway in ESC (Mayor-Ruiz et al., 2018). Remarkably, we showed that deletion of ERF in RAS deficient cells ($RAS^{KO}ERF^{KO}$) rescued their proliferation and differentiation related defects (Mayor-Ruiz et al., 2018). However, the molecular mechanism underlying this rescue and the precise role of ERF during early embryonic development and pluripotent transitions remained unclear. Identifying this precise mechanism is the goal of this Thesis.

To address these important questions, we first analyzed the expression pattern of ERF during early embryonic development. For this, we collected mouse embryos at different developmental stages and performed immunofluorescence analyses. We determined that ERF expression peaks around E3.5-E4.0 (Figure 6A), a period of time where the epiblast resides in a naïve state of pluripotency (Nichols and Smith, 2012, Weinberger et al., 2016). We observed that ERF is expressed in both, ICM and TE, while it is negligible in the PrE (Figure 6B-E). The expression of ERF in the TE is consistent with its reported requirement for chorionic trophoblast differentiation (Vorgia et al., 2017). Nevertheless, we focused on its expression in the ICM as ESC are isolated from this group of cells. We observed that ERF expression correlated with the expression of the naïve pluripotent markers NANOG and KLF4 (Figure 6B-E). Indeed, exit from naïve pluripotency *in vivo* and downregulation of naïve associated markers strongly correlated with decreased ERF expression (Figure 6B, C). We confirmed this observation by quantifying the levels of ERF and the naïve markers NANOG and KLF4 at a single nuclei level (Figure 6E). We also validated the observed expression pattern for ERF by analyzing single-cell transcriptomes from mouse embryos at different developmental stages where ERF expression is also downregulated upon lineage commitment to PrE or EPI (Figure 7) (Nowotschin et al., 2019). Combined, these results showed that the expression of ERF is upregulated during ICM specification, and it is quickly downregulated before implantation, suggesting a role for ERF in the naïve pluripotent epiblast.

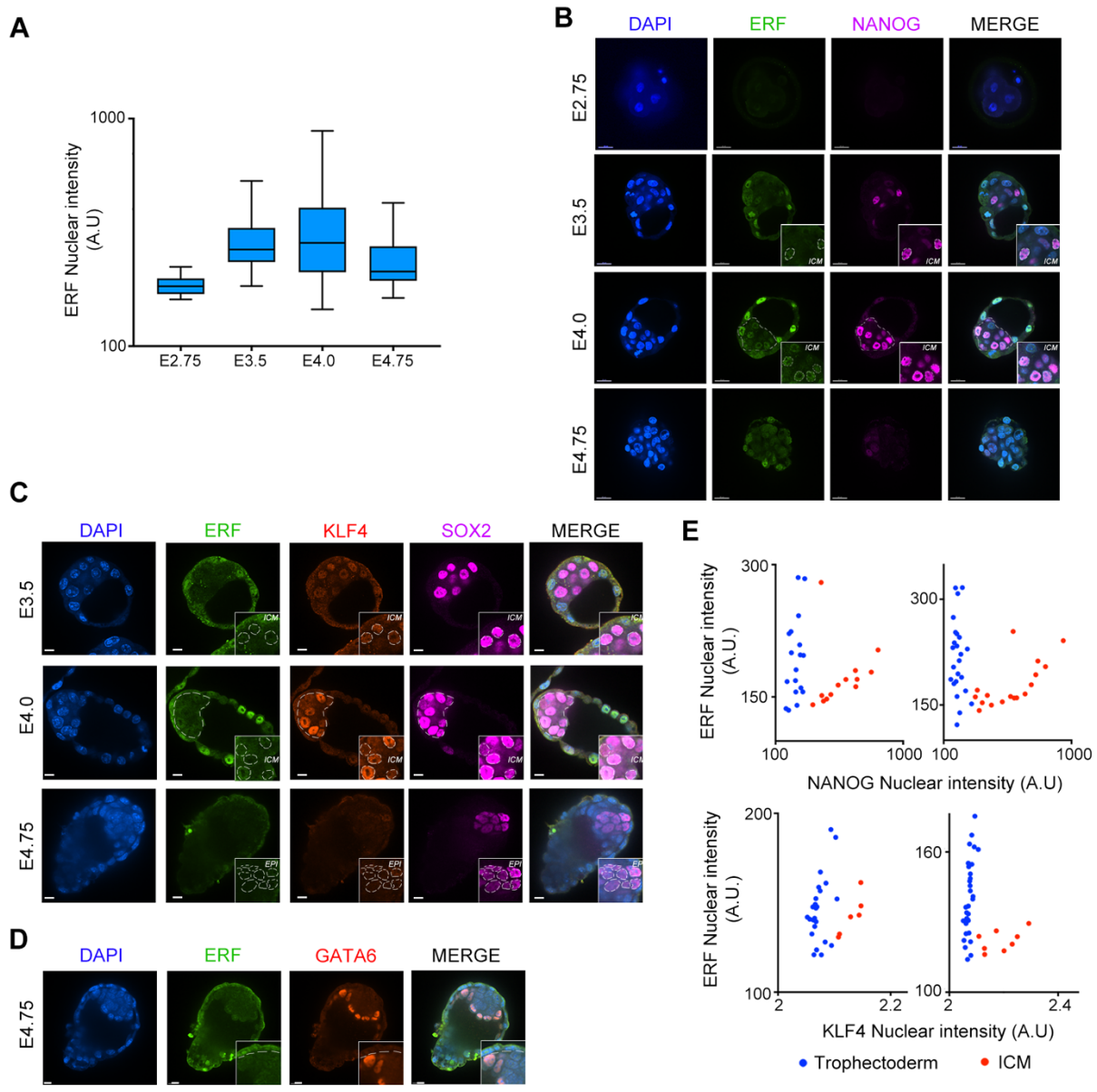


**Figure 6. ERF expression correlates with naïve pluripotent markers. A**: Graph showing ERF mean nuclear fluorescent intensity in mouse embryos at different stages of embryonic development. All cells from the embryo were considered when generating this plot. The number of embryos and cells used for this quantification is described in Materials and Methods. (A.U.: arbitrary units). **B**: Immunofluorescence analysis of NANOG and ERF in mouse embryos at E2.75, E3.5, E4.0 and E4.75. Dashed line highlights the ICM. DAPI was used to visualize nuclei. Scale bars, 20μm. **C**: Immunofluorescence analysis of KLF4, SOX2 and ERF in mouse embryos at E3.5, E4.0 and E4.75. Dashed line highlights the ICM/EPI. DAPI was used to visualize nuclei. Scale bars, 20μm. **D**: Immunofluorescence analysis of GATA6, NANOG and ERF in mouse embryos at E4.75. DAPI was used to visualize nuclei. Scale bars, 20μm. **E**: Graphs showing relative nuclear fluorescence intensity of ERF and NANOG (upper panel) and ERF and KLF4 (lower panel). Every dot represents one single nucleus, and each plot corresponds to an individual E3.5 embryo. Two representative examples are shown but at least 10 embryos were analyzed.

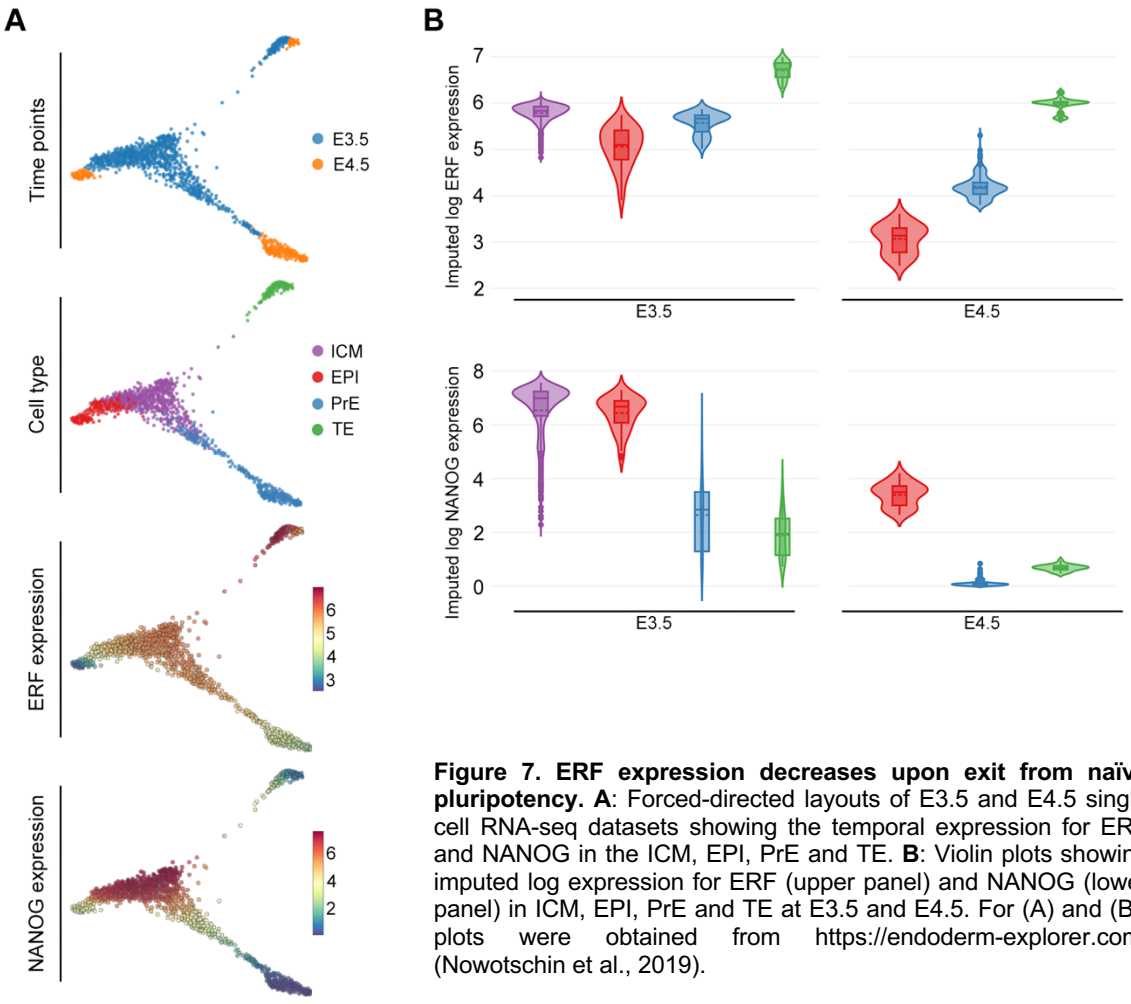


**Figure 7. ERF expression decreases upon exit from naïve pluripotency. A**: Forced-directed layouts of E3.5 and E4.5 single cell RNA-seq datasets showing the temporal expression for ERF and NANOG in the ICM, EPI, PrE and TE. **B**: Violin plots showing imputed log expression for ERF (upper panel) and NANOG (lower panel) in ICM, EPI, PrE and TE at E3.5 and E4.5. For (A) and (B), plots were obtained from https://endoderm-explorer.com/ (Nowotschin et al., 2019).

In order to validate these observations *in vivo* and further assess the role of the MAPK pathway in ERF levels, we used our mouse ESC model ($RAS^{lox/lox}$) to examine the transition from naïve to primed pluripotency (Mayor-Ruiz et al., 2018, Drosten et al., 2010). Thus, we induced the transition of naïve ESC growing in 2i+LIF (2iL) conditions, to primed EpiLC with FGF2 and Activin A (FA) and examined ERF levels (Hayashi et al., 2011, Nakaki et al., 2013). $RAS^{lox/lox}$ and RAS-deficient cells ($RAS^{KO}$) maintained in naïve conditions (2iL) showed high levels of ERF as well as the naïve marker NANOG (Figure 8A). However, two days after differentiation, FA-$RAS^{lox/lox}$ showed negligible levels of ERF (Figure 8A). During this transition, ERF is quickly phosphorylated and translocated to the cytoplasm along with a decrease in the protein levels due to transcriptional repression (Figure 8B) (Yang et al., 2019, Martinez-Val et al., 2021). On the contrary, FA-$RAS^{KO}$ retained elevated levels of ERF, as well as NANOG, after differentiation

suggesting that ERF downregulation depended on FGF/MAPK activation (Figure 8A). Combined, these results pointed to a role for ERF in the exit from naïve pluripotency in a MAPK-dependent manner.

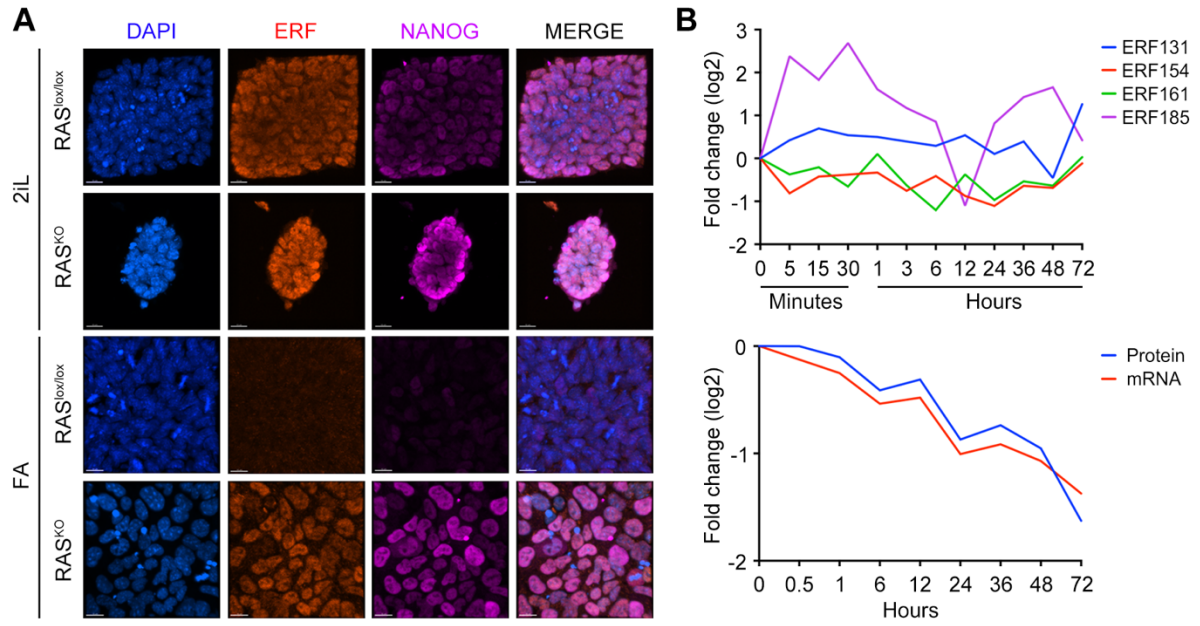


**Figure 8. Exit from naïve pluripotency correlates with decreased levels of ERF. A**: Immunofluorescence analysis performed in 2iL- and FA-treated $RAS^{lox/lox}$ and $RAS^{KO}$ ESC to detect ERF and NANOG. DAPI was used to visualize nuclei. Scale bars, 15µm. **B**: Temporal dynamics of relative ERF phosphorylation levels at specific phospho-sites (upper panel) and ERF protein and mRNA levels (lower panel) during the transition from ESC to EpiLC. Data was obtained from (Yang et al., 2019).

## Downregulation of ERF is necessary for the successful exit from naïve pluripotency in the absence of RAS signaling

To evaluate the implication of ERF in the exit from naïve pluripotency, we examined rosette formation and lumenogenesis using the genetic ESC models described above. In this assay, individual ESC that are embedded in an extracellular matrix (Matrigel) and withdrawn of 2iL, exit from naïve pluripotency, divide and self-organize into polarized rosettes with a single lumen in the center of the spheroid. Rosette polarization and lumenogenesis are examined by the expression of podocalyxin (PDX), an apical membrane protein, and/or by localization of phalloidin, peptide that binds to the actin cytoskeleton and highly enriched in the lumen. All this process mimics the morphogenic events of the epiblast during embryo implantation (Bedzhov and Zernicka-Goetz, 2014). Importantly, embryonic rosettes generated in the presence of 2iL lack

lumen, maintain the expression of naïve markers and become disorganized over time (Shahbazi et al., 2017). These observations demonstrated that the exit from naïve pluripotency is necessary for successful polarization and cavity formation.

To analyze whether ERF regulates the exit from naïve pluripotency, we generated ERF knockouts in the ESC model by CRISPR-mediated editing and evaluated the rosette formation in all different genotypes ($RAS^{lox/lox}$, $RAS^{KO}$, $ERF^{KO}$ and $RAS^{KO}ERF^{KO}$). Upon 2iL removal and suspension in Matrigel, $RAS^{lox/lox}$ rosettes showed clear polarization and lumen, expression of PDX and downregulation of the naïve marker NANOG (Figures 9 and 10). Deletion of ERF in $RAS^{lox/lox}$ ($ERF^{KO}$) did not affect the formation of rosettes (Figures 9 and 10). However, $RAS^{KO}$ ESC failed to form rosettes and developed into a disorganized group of cells that maintained elevated expression of NANOG (Figures 9 and 10). Importantly, elimination of ERF in $RAS^{KO}$ ESC was sufficient to induce the exit from naïve pluripotency and rescue the failed morphogenic events of polarization and lumenogenesis (Figures 9 and 10).

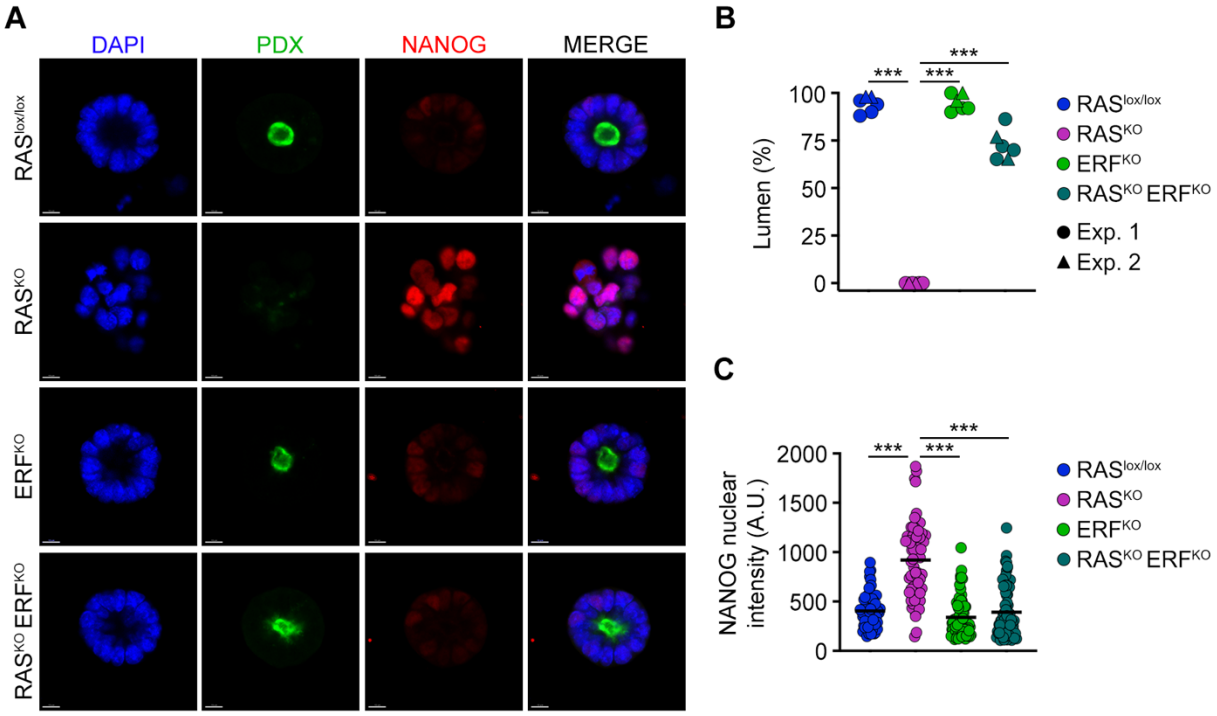


**Figure 9. Successful exit from naïve pluripotency requires downregulation of ERF in the absence of RAS signaling. A**: Central confocal optical sections of $RAS^{lox/lox}$, $ERF^{KO}$, $RAS^{KO}$, and $RAS^{KO}ERF^{KO}$ embryonic cell rosettes embedded in Matrigel 48 hours after seeding and stained for NANOG and PDX. DAPI was used to visualize nuclei. Scale bars, 10µm. **B**: Graph showing the percentage of embryonic rosettes generating a lumen (PDX+) in all genotypes. Data comes from (A). Two independent experiments are shown and at least, a total of 50 rosettes were counted per sample. ***=p<0.001, t-student. **C**: Graph showing mean NANOG nuclear fluorescence intensity per nucleus in embryonic rosettes 48 hours after seeding. One representative experiment is shown and a total of 70 nuclei from different rosettes were counted per sample. ***=p<0.001, t-student.

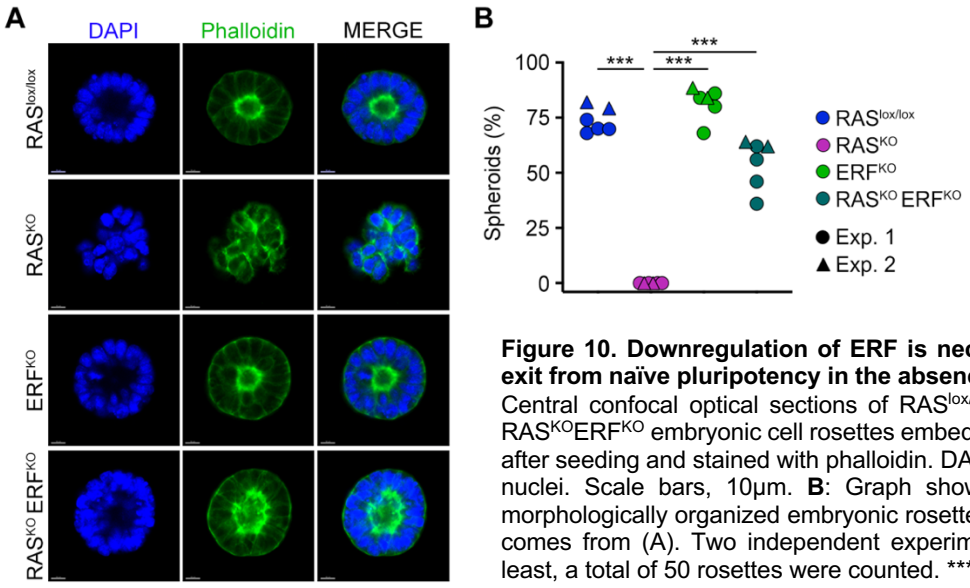


**Figure 10. Downregulation of ERF is necessary for successful exit from naïve pluripotency in the absence of RAS signaling**. **A**: Central confocal optical sections of $RAS^{lox/lox}$, $ERF^{KO}$, $RAS^{KO}$, and $RAS^{KO}ERF^{KO}$ embryonic cell rosettes embedded in Matrigel 48 hours after seeding and stained with phalloidin. DAPI was used to visualize nuclei. Scale bars, 10µm. **B**: Graph showing the percentage of morphologically organized embryonic rosettes in all genotypes. Data comes from (A). Two independent experiments are shown and at least, a total of 50 rosettes were counted. ***=p<0.001, t-student.

It has been shown that WNT inhibition promotes rosette formation while further MEK inhibition promotes lumen formation (Neagu et al., 2020). Thus, it is possible that $RAS^{KO}$ ESC still retain elevated levels of WNT signaling when placed in Matrigel, which will impair rosette formation. To examine whether $RAS^{KO}$ ESC have the ability to form rosettes, we cultured $RAS^{lox/lox}$ and $RAS^{KO}$ ESC with or without the WNT inhibitor IWR-1. While $RAS^{lox/lox}$ ESC still developed embryonic rosettes, $RAS^{KO}$ ESC are unable to organize a rosette even in the absence of WNT signaling suggesting that RAS signaling is necessary for both, rosette and lumen formation (Figure 11).

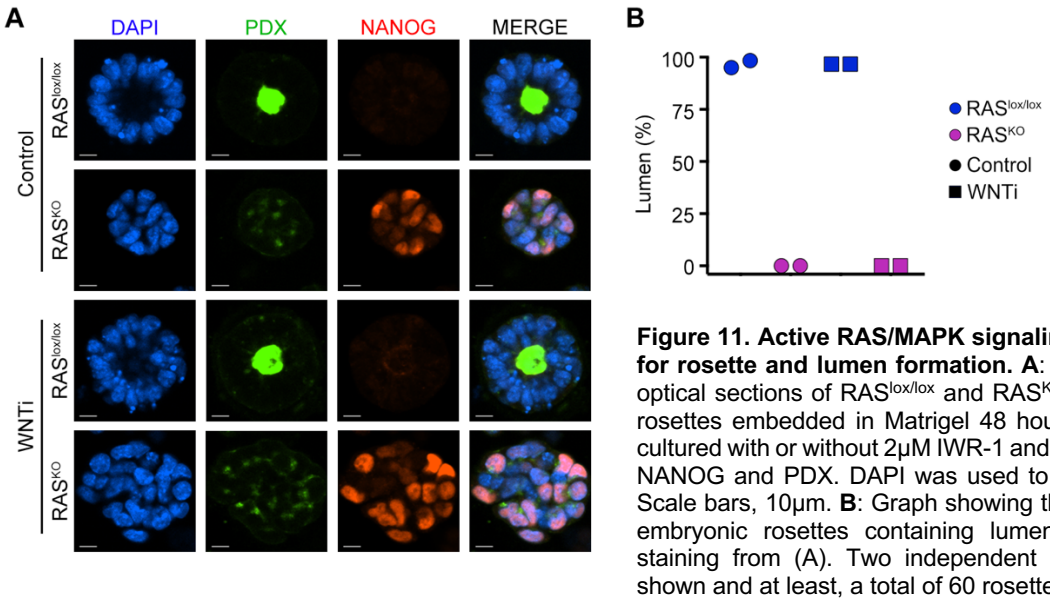


**Figure 11. Active RAS/MAPK signaling is necessary for rosette and lumen formation. A**: Central confocal optical sections of $RAS^{lox/lox}$ and $RAS^{KO}$ embryonic cell rosettes embedded in Matrigel 48 hours after seeding cultured with or without 2µM IWR-1 and stained to detect NANOG and PDX. DAPI was used to visualize nuclei. Scale bars, 10µm. **B**: Graph showing the percentage of embryonic rosettes containing lumen based on the staining from (A). Two independent experiments are shown and at least, a total of 60 rosettes were counted.

To further support these observations, we generated knock-in reporter cell lines in all genotypes ($RAS^{lox/lox}$, $RAS^{KO}$, $ERF^{KO}$ and $RAS^{KO}ERF^{KO}$) by CRISPR-mediated editing (REX1-deGFP), in which the endogenous coding sequence of the naïve marker REX1 (also known as ZFP42) was replaced with a short half-life form of eGFP (destabilized eGFP or deGFP). Similar REX1-deGFP reporter ESC have been extensively used as a faithful system to monitor exit from naïve pluripotency (Kalkan et al., 2017). Upon differentiation to EpiLC by FA, $RAS^{lox/lox}$ and $ERF^{KO}$ ESC showed efficient deGFP downregulation (Figure 12A). In contrast, FA-$RAS^{KO}$ did not show signs of deGFP downregulation (Figure 12A). Conversely, exit from naïve pluripotency was efficiently achieved in FA-$RAS^{KO}ERF^{KO}$ (Figure 12A).

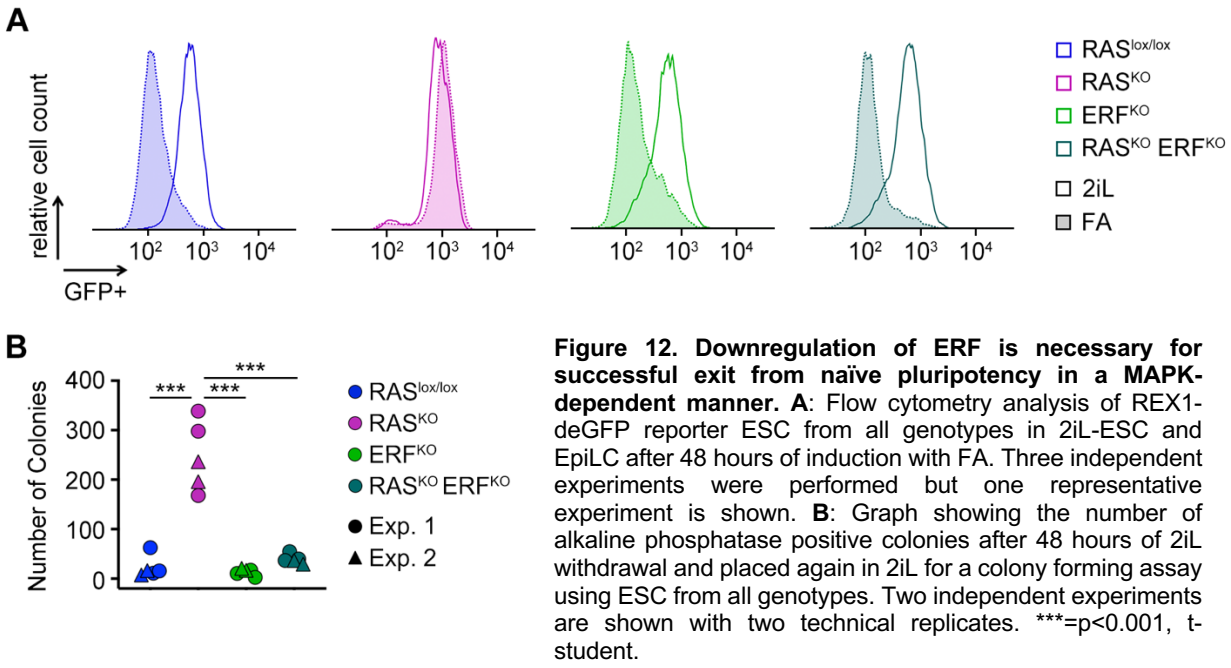


**Figure 12. Downregulation of ERF is necessary for successful exit from naïve pluripotency in a MAPK-dependent manner. A**: Flow cytometry analysis of REX1-deGFP reporter ESC from all genotypes in 2iL-ESC and EpiLC after 48 hours of induction with FA. Three independent experiments were performed but one representative experiment is shown. **B**: Graph showing the number of alkaline phosphatase positive colonies after 48 hours of 2iL withdrawal and placed again in 2iL for a colony forming assay using ESC from all genotypes. Two independent experiments are shown with two technical replicates. ***=p<0.001, t-student.

Finally, we also analyzed the clonogenicity and self-renewal capacity of our ESC lines by withdrawing 2iL from the culture media for 48 hours and plating back these ESC at clonal density in 2iL conditions. During this 2iL withdrawal, cells that exit naïve pluripotency are irreversibly committed and lose the ability to generate colonies with naïve morphology in 2iL conditions. Indeed, this was the case for $RAS^{lox/lox}$ and $ERF^{KO}$ ESC (Figure 12B). Conversely, $RAS^{KO}$ were able to generate undifferentiated naïve-like ESC colonies (evaluated by alkaline phosphatase staining) suggesting that remained trapped in a naïve pluripotent state, ability that was

extinguished in $RAS^{KO}ERF^{KO}$ ESC (Figure 12B). Collectively, our results revealed a predominant role for ERF controlling the exit from naïve pluripotency in a MAPK-dependent manner.

## ERF regulates the transition from naïve to primed pluripotency in a MAPK-dependent manner

To investigate the molecular mechanisms underlying the rescue mediated by the loss of ERF during the exit from naïve pluripotency, we performed RNA-seq analysis of our ESC ($RAS^{lox/lox}$, $RAS^{KO}$, $ERF^{KO}$ and $RAS^{KO}ERF^{KO}$) cultured in naïve conditions (2iL) and differentiated to EpiLC with FA treatment. Principal component analysis (PCA) segregated the samples based on their differentiation status, separating naïve from primed pluripotent states alongside principal component 1 (PC1) and MAPK activity alongside PC2 (Figure 13A). Interestingly, FA-$RAS^{KO}$ are localized in an intermediate state between naïve and primed pluripotency, characterized by the expression of both naïve pluripotent markers, such as NANOG, and primed associated genes including OTX2 (Figure 13A-C). Indeed, while naïve pluripotent ESC are characterized by a $NANOG^{+}/OTX2^{-}/OCT6^{-}$ state and primed pluripotent cells by $NANOG^{-}/OTX2^{+}/OCT6^{+}$, FA-$RAS^{KO}$ showed a $NANOG^{+}/OTX2^{+}/OCT6^{-}$ state (Figure 13B, C). Furthermore, consistent with our observations above, we detected high levels of ERF in FA-$RAS^{KO}$, while negligible in FA-$RAS^{lox/lox}$ (Figure 13C). Interestingly, FA-$RAS^{KO}$ ESC co-express OTX2, ERF and NANOG showing heterogenous levels between individual cells (Figure 13D).

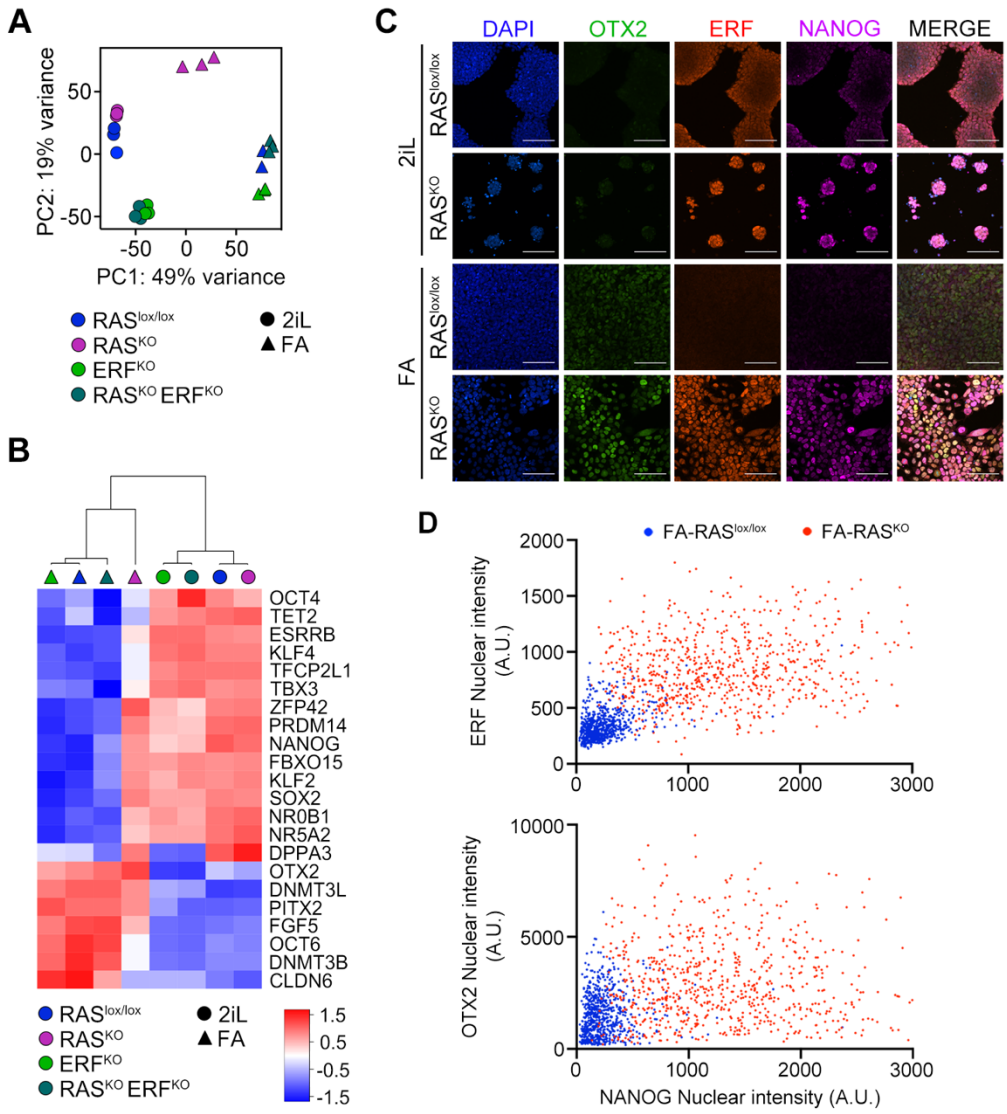


**Figure 13. ERF controls the transition to primed pluripotency in a MAPK-dependent manner. A**: PCA plot generated from RNA-seq data of RAS$^{lox/lox}$, ERF$^{KO}$, RAS$^{KO}$, and RAS$^{KO}$ERF$^{KO}$ ESC cultured in 2iL or induced to differentiate to EpiLC (FA) for 48 hours. Three replicates per condition are shown. **B**: Heatmap generated from the RNA-seq data described in (A) showing the average from the three replicates. **C**: Immunofluorescence analysis of 2iL and FA treated RAS$^{lox/lox}$ and RAS$^{KO}$ ESC stained for OTX2, ERF and NANOG. DAPI was used to visualize nuclei. Scale bars, 100µm. **D**: Graph plots showing quantified expression levels of NANOG/ERF (upper panel) and OTX2/NANOG (lower panel) in FA-RAS$^{lox/lox}$ and FA-RAS$^{KO}$ ESC. Number of cells: 750.

In order to further characterize the intermediate state of FA-RAS$^{KO}$, we used available datasets that evaluate temporal transcriptional dynamics during the transition from naïve to primed pluripotency and determined that FA-RAS$^{KO}$ resembled transcriptionally to ESC primed with FA for 12-24 hours (Figure 14A, B) (Yang et al., 2019). Interestingly, FA-RAS$^{KO}$ ESC are reminiscent of the recently described intermediate pluripotent states, rosette and formative

pluripotent states (RSC, FSC, XPSC and fPSC) (Neagu et al., 2020, Kinoshita et al., 2020, Yu et al., 2020, Wang et al., 2021). To explore whether FA-RAS$^{KO}$ ESC are transcriptionally similar to these intermediate pluripotent states we analyzed our RNA-seq data in the context of those corresponding to rosette and formative pluripotency (Neagu et al., 2020, Kinoshita et al., 2020, Yu et al., 2020, Wang et al., 2021) and performed a PCA analysis. In this analysis, samples segregated again based on their differentiation status alongside principal component 1 (PC1) and placed all intermediate pluripotent states in a similar transcriptional space (Figure 14C). However, PC2 clearly separated FA-RAS$^{KO}$ ESC from rosette and formative pluripotent states (Figure 14C). Hierarchical clustering analysis based on the expression of defined naïve and primed markers showed that RSC and FA-RAS$^{KO}$ ESC are transcriptionally more comparable, likely to the defective MAPK signaling, either chemically (RSC) or genetically (FA-RAS$^{KO}$ ESC), in both intermediate states (Figure 14D).

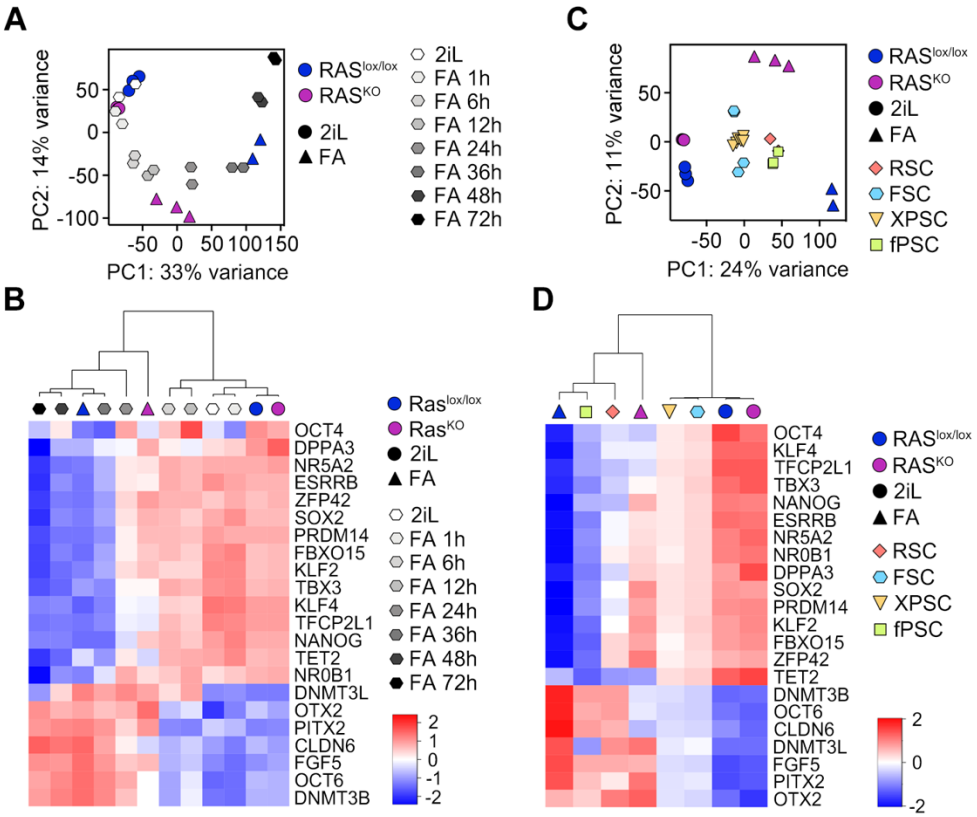


**Figure 14. FA-RAS$^{KO}$ cells reside in an intermediate state of pluripotency. A**: PCA plot generated from RNA-seq datasets (three replicates) showing 2iL and FA treated RAS$^{lox/lox}$ and RAS$^{KO}$ ESC together with RNA-seq datasets (two replicates) from a time course experiment during EpiLC induction (0, 1, 6, 12, 24, 36, 48 and 72 hours) (Yang et al., 2019). **B**: Heatmap generated from RNA-seq data from samples described in (A) showing the averaged values of at least 2 replicates. **C**: PCA plot generated from RNA-seq datasets showing 2iL and FA treated RAS$^{lox/lox}$ and RAS$^{KO}$ ESC together with RNA-seq datasets from RSC, FSC, fPSC and XPSC (Neadu et al., 2020, Kinoshita et al., 2020, Yu et al., 2020, Wang et al., 2021). At least two replicates are shown. **D**: Heatmap generated from RNA-seq data from samples described in (C) showing the average from two or three replicates as applicable to each sample.

Finally, since differentiation of ESC to EpiLC resulted in eventual cell death unless they are further differentiated to PGC, we analyzed the capacity of propagation and maintenance over time of the FA-RAS$^{KO}$ ESC, which reside in an intermediate pluripotent state. For this, we examined whether FA-RAS$^{KO}$ cells could be propagated in culture under FGF2/Activin-A/XAV939 conditions (FAX). Indeed, we observed that FA-RAS$^{KO}$ cells could be stably maintained in culture for more than 15 passages, while RAS$^{lox/lox}$, ERF$^{KO}$ and RAS$^{KO}$ERF$^{KO}$ ESC failed to propagate (Figure 15A). Consistently, RAS$^{KO}$ cells in FAX conditions retained the expression of naïve pluripotent markers as well as ERF and the primed associated gene OTX2 demonstrating that they could be propagated over time while maintaining their intermediate characteristics (Figure 15B). Cultured FAX-RAS$^{KO}$ ESC also showed heterogenous levels of OTX2, ERF and NANOG between individual cells suggesting that these cells might fluctuate between different transcriptional states. Importantly, FAX-RAS$^{KO}$ ESC can revert back to a naïve pluripotent state when transferred back to 2iL conditions demonstrating that this intermediate state is reversible (Figure 16).

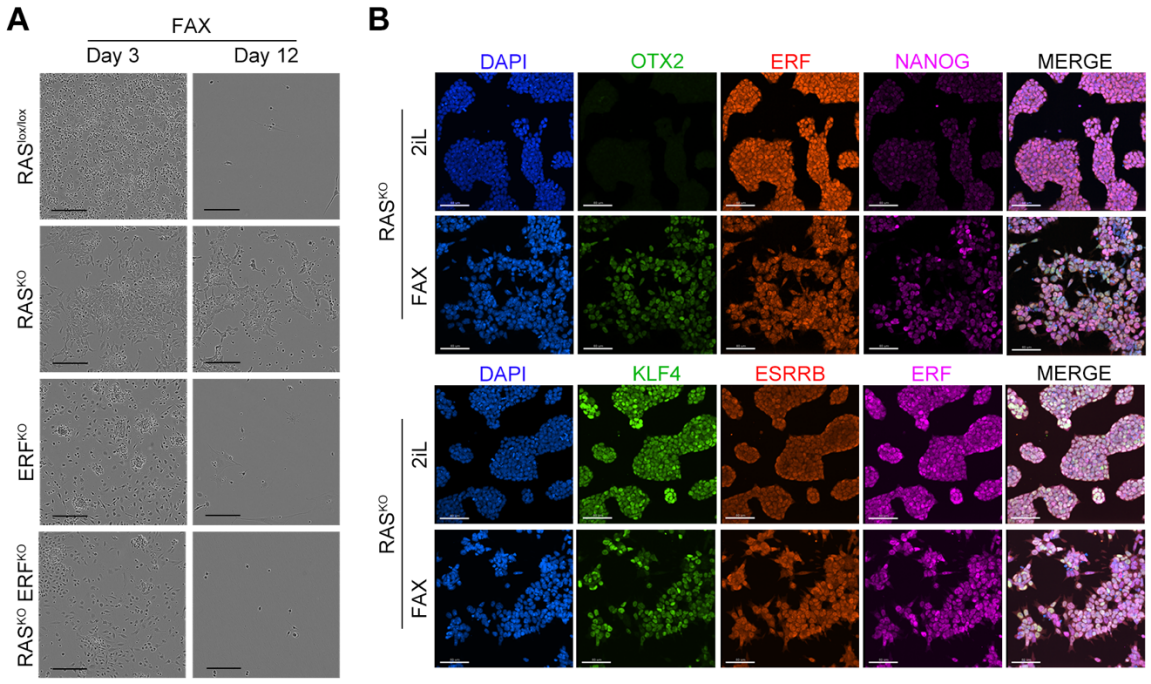


**Figure 15. FAX-RAS$^{KO}$ cells can be stably maintained in culture. A**: Bright field images of RAS$^{lox/lox}$, ERF$^{KO}$, RAS$^{KO}$, and RAS$^{KO}$ERF$^{KO}$ ESC cultures in EpiLC media (FAX) 3 and 12 days after the media switch. Scale bars, 200µm. **B**: Immunofluorescence analysis of 2iL and FAX treated RAS$^{KO}$ ESC and stained for OTX2, ERF and NANOG are shown. DAPI was used to visualize nuclei. Scale bars, 80µm.

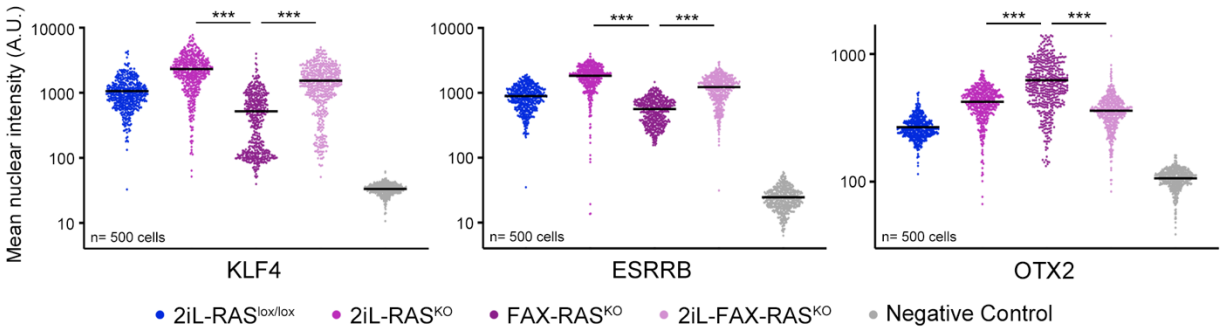


**Figure 16. The intermediate pluripotent state in FA-RAS$^{KO}$ ESC is reversible.** High-throughput imaging (HTI) quantification of the mean nuclear intensity for KLF4 (left), ESRRB (center) and OTX2 (right) in 2iL-RAS$^{lox/lox}$, 2i-RAS$^{KO}$, FAX-RAS$^{KO}$ and 2iL-FAX-RAS$^{KO}$ (FAX-growing ESC transferred to 2iL conditions) ESC. Data are representative of at least two independent clones. Center lines indicate mean values. *** = p<0.001. t-student. Negative control indicates no primary antibody. Number of cells: 500.

Finally, our results further demonstrated that loss of ERF is necessary and sufficient to overcome the developmental blockage of FA-RAS$^{KO}$ cells in their intermediate pluripotent state. Indeed, RNA-seq data revealed that deletion of ERF in FA-RAS$^{KO}$ cells (RAS$^{KO}$ERF$^{KO}$) restored the overall gene expression profile to be indistinguishable from FA-RAS$^{lox/lox}$ cells (Figure 13A, B). In summary, our data point to ERF as the MAPK-dependent switch that triggers full commitment to primed pluripotency upon RAS activation.

## Chromatin-bound ERF at enhancers ensures an optimal naïve pluripotent state

As shown above, the expression of ERF correlates with high levels of naïve pluripotent markers *in vivo* and *in vitro* and is quickly downregulated upon induction to primed pluripotency (Figures 6 and 7). In our previous work, we showed that ERF was enriched in a total of 2074 bona-fide ESC enhancers identified in RAS$^{KO}$ ESC (2074/5529 total ERF peaks) (Figure 17A). Among these, ERF binds to most of the super-enhancers identified in ESC (198/231) (Mayor-Ruiz et al., 2018, Hnisz et al., 2013, Whyte et al., 2013). The super-enhancers where ERF binds are associated to highly transcribed naïve pluripotent genes (PRDM14, ZFP42, KLF4, ESRRB, NANOG or TBX3) as well as to general pluripotent transcription factors (OCT4 or SOX2) (Figure

17B). Based on these observations and, although ERF is considered to be a transcriptional repressor, we hypothesized that ERF might play a different role at ESC enhancers.

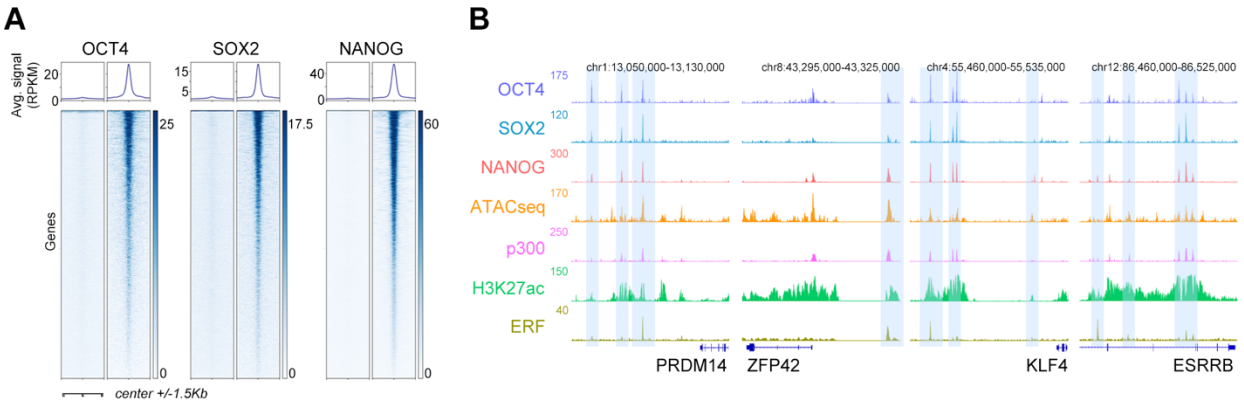


**Figure 17. ERF binds to enhancers and super-enhancers in ESC. A**: Heatmaps showing OCT4, SOX2 and NANOG (Galonska et al., 2015) enrichment at the set of 5529 ERF-bound sites. **B**: Genome browser tracks showing OCT4, SOX2, NANOG (Galonska et al., 2015), H3K27ac, P300 (Buecker et al., 2014), ATAC-seq (Wu et al., 2016) and ERF (Mayor-Ruiz et al., 2018) normalized read count at PRDM14, ESRRB, KLF4 and REX1 (ZFP42) naïve pluripotent genes in ESC. ERF binding sites are highlighted.

To explore the relevance of ERF at these sites, we first examined the level of occupancy of the pluripotent transcription factors OCT4, SOX2 and NANOG in the 2074 ERF-binding sites at ESC enhancers (Datasets from (Galonska et al., 2015)). We observed that the enrichment of these factors at the 2074 ERF-bound enhancers is higher compared to a non-ERF bound randomized set of 2074 different enhancers (Figure 18A). In addition, ERF-bound ESC enhancers are also characterized by higher H3K27Ac levels, increased p300 binding and chromatin accessibility detected by ATAC-seq, all of them, markers of active enhancers (Figure 18B) (Datasets from (Buecker et al., 2014, Wu et al., 2016). These results suggested that ERF binding at enhancers correlated with the activity of these enhancers, and consequently, might influence the expression of their associated genes. Therefore, we analyzed the expression levels of essential naïve pluripotent genes associated to ERF-bound super-enhancers (NANOG, PRDM14, ZFP42, TBX3, KLF4 and ESRRB) in $RAS^{lox/lox}$ and $ERF^{KO}$ ESC grown in 2iL conditions using our RNA-seq data. Interestingly, NANOG, PRDM14 and ZFP42 showed decreased expression in $ERF^{KO}$ ESC while TBX3, KLF4 and ESRRB did not show any change (Figure 19A). This suggested that ESC enhancers at specific genomic locations might be less active in the absence of ERF. To confirm that ERF-bound enhancers are less active in $ERF^{KO}$ ESC compare to $RAS^{lox/lox}$, we cloned the three ERF-bound enhancer regions controlling PRDM14 gene expression in GFP

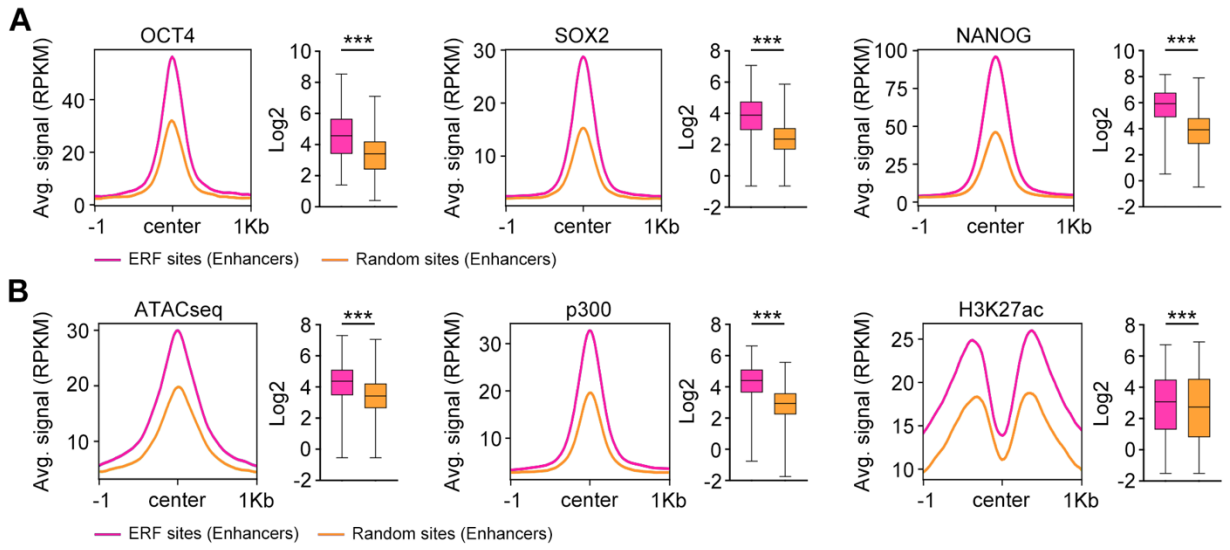


**Figure 18. ERF binding is associated to highly active ESC enhancers. A**: ChIP-seq read density plot (RPKM) showing OCT4, SOX2 and NANOG enrichment at the 2074 ERF-binding sites at enhancers or at a set of 2074 randomly selected non-ERF bound enhancers. Graphs show quantifications of the TF enrichment in each set of sites. *** = p<0.001, t-student. Data was obtained from (Galonska et al., 2015). **B**: ChIP-seq read density plot showing H3K27ac, p300 (Buecker et al., 2014), as well as ATAC-seq signal (Wu et al., 2016) at the same binding sites described in (A). *** = p<0.001, t-student.

reporter PiggyBac constructs (see Figure 20B to visualize the enhancers). Transfection of these GFP reporter constructs in $RAS^{lox/lox}$ and $ERF^{KO}$ ESC demonstrated that the activity of these enhancers was lower in $ERF^{KO}$ ESC (Figure 19B) and suggested that ERF promoted enhancer activity. Next, we hypothesized that reduced levels of NANOG in $ERF^{KO}$ ESC could affect the expression of naïve-associated genes. Indeed, it has been reported that NANOG promotes chromatin accessibility and binding of additional pluripotent factors to enhancers, maintaining naïve pluripotency and self-renewal in ESC (Heurtier et al., 2019). Accordingly, $ERF^{KO}$ cells showed decreased expression of a subset of genes characteristic of the naïve pluripotent transcriptional network (Figure 19C). Consistent with these results, by generating a unidimensional PCA plot, which segregated samples based on their differentiation status (PC1), we observed that 2iL-$ERF^{KO}$ are biased toward differentiation compared to control 2iL-$RAS^{lox/lox}$ ESC (Figure 19D). These combined results revealed that ESC growing under naïve conditions required ERF to maintain an optimal naïve pluripotent state.

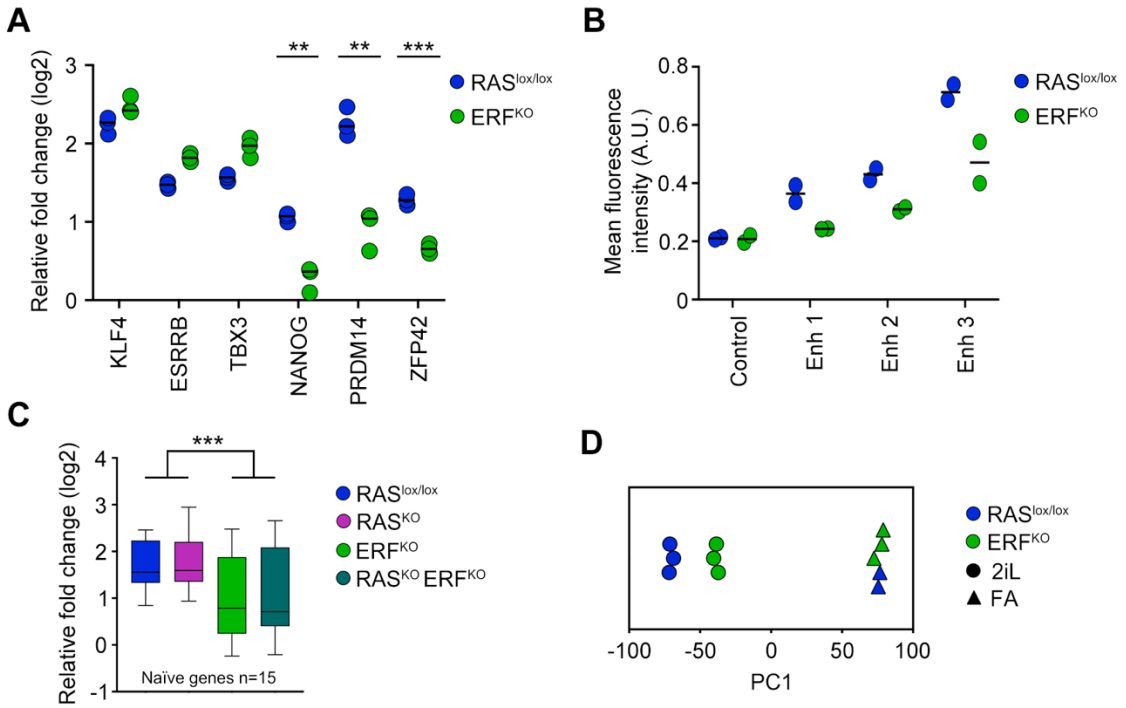


**Figure 19. ERF regulates the expression of naïve pluripotent transcription factors in ESC. A**: Graph showing relative fold change (log2) expression of the indicated genes in RAS$^{lox/lox}$ and ERF$^{KO}$ ESC grown in 2iL. For each gene, data was normalized to the average across all samples. *** = p<0.001; ** = p<0.01. t-student. Data is shown as triplicates and was obtained from RNA-seq datasets. **B**: Graph showing mean fluorescence intensity (GFP) measured by flow cytometry from RAS$^{lox/lox}$ and ERF$^{KO}$ ESC cultured in 2iL and transfected with the corresponding reporter PiggyBac constructs. PRDM14 enhancer regions drive the expression of GFP. A plasmid with a constitutive promoter expressing mCherry was used to normalize the GFP signal. Two independent experiments were performed in two ESC clones but only one is shown. **C**: Graph showing the relative fold change (log2) expression of a subset of 15 naïve associated genes (*Klf4, Esrrb, Tfcp2l1, Tbx3, Klf2, Elf3, Klf8, Nanog, Prdm14, Tcl1, Zfp42, Nrob1, Prmd16, Dazl and Crxos*) in the different genotypes in 2iL conditions. For each gene, data was normalized to the average across all samples and was obtained from RNA-seq datasets. *** = p<0.001. t-student. **D**: Unidimensional PCA plot of RNA-seq data of RAS$^{lox/lox}$ and ERF$^{KO}$ ESC cultured in 2iL or induced to differentiate (FA) during 48 hours to EpiLC. Three replicates per condition are shown. PC1 separates samples by differentiation status.

Finally, to confirm our observations, we performed a CUT&RUN analysis for SOX2 and NANOG to evaluate their enrichment at enhancers in RAS$^{lox/lox}$ and ERF$^{KO}$ ESC grown in 2iL conditions. As predicted, both pluripotent transcription factors showed an overall decreased enrichment in ERF-bound enhancers as well as in all ESC enhancers in 2iL-ERF$^{KO}$ ESC (Figure 20). These data supported our findings and revealed an unexpected unique role for ERF to maintain an optimal level of naïve pluripotency.

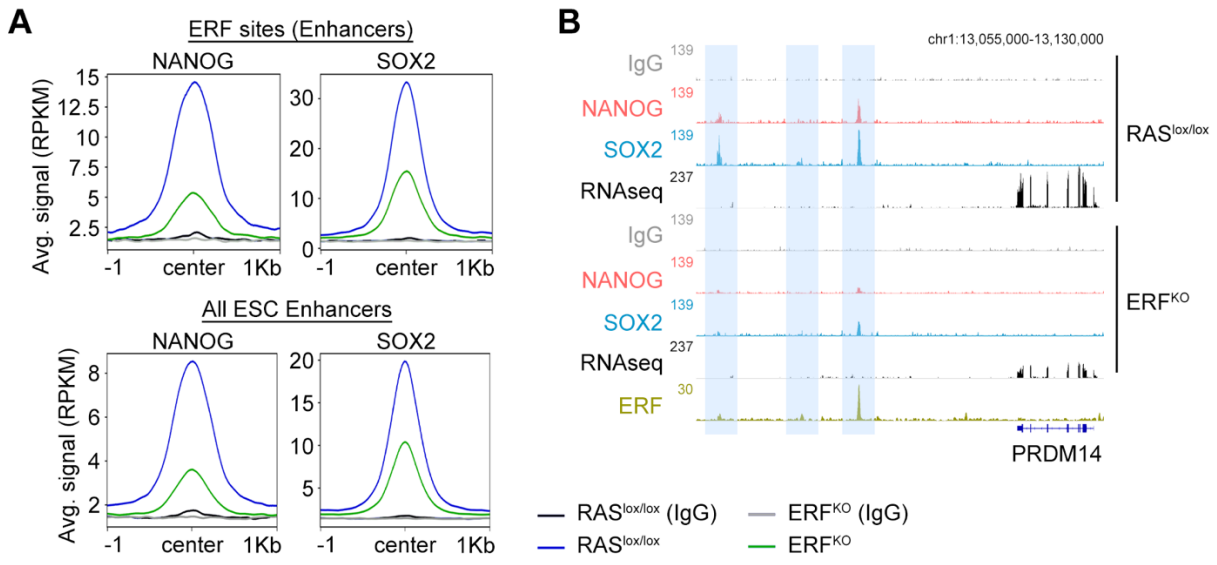


**Figure 20. ERF ensures optimal naïve pluripotent transcription factor enrichment and expression in ESC. A**: CUT&RUN read density plot (RPKM) showing NANOG and SOX2 enrichment in the set of 2074 ERF-binding sites at enhancers and all ESC enhancers in $RAS^{lox/lox}$ and $ERF^{KO}$ ESC cultured in 2iL. Corresponding inputs (IgG) are also shown as reference control. **B**: Genome browser tracks showing NANOG and SOX2 enrichment and RNA-seq RPKM read count at the PRDM14 gene in the indicated genotypes. ERF binding profile in $RAS^{KO}$ ESC is also shown. Inputs (IgG) are also shown as a reference control. ERF binding sites are highlighted.

## The naïve enhancer landscape is active in FA-$RAS^{KO}$ ESC

The transition from naïve to primed pluripotency is associated to a global reorganization of OCT4 genomic binding. Indeed, OCT4 shifts from enhancers associated with key players in naïve pluripotency and engages in new enhancers of genes implicated in post-implantation development (Buecker et al., 2014). Decommission of naïve enhancers and consequent downregulation of the associated transcription factors, including ESRRB, KLF4 or NANOG, is necessary for the successful progression to primed pluripotency. Using publicly available datasets for OCT4 occupancy in ESC and EpiLC and based on the relative occupancy between both pluripotent states, we defined the top OCT4 sites preferentially enriched in ESC (4759 sites, $OCT4^{ESC}$), EpiLC (2921 sites, $OCT4^{EpiLC}$) and commonly shared between the two (9144 sites, $OCT4^{Common}$) (Figure 21A). Genes associated with $OCT4^{ESC}$ sites are mostly downregulated during the transition to primed pluripotency whereas genes associated to $OCT4^{EpiLC}$ sites are upregulated (Buecker et al., 2014). We next examined how many of these OCT4 sites were also co-occupied by ERF and we determined a total of 12.52% in $OCT4^{ESC}$ (596/4759 sites,

ERF/OCT4$^{ESC}$), 13.62% in OCT4$^{Common}$ (1246/9144 sites, ERF/OCT4$^{Common}$) and 0.15% in OCT4$^{EpiLC}$ (44/2921 sites, ERF/OCT4$^{EpiLC}$) (Figure 21B). This analysis suggested that ERF does not play a specific role in genes associated with EpiLC-specific sequences but instead in regulating OCT4$^{ESC}$ and OCT4$^{Common}$ sites.

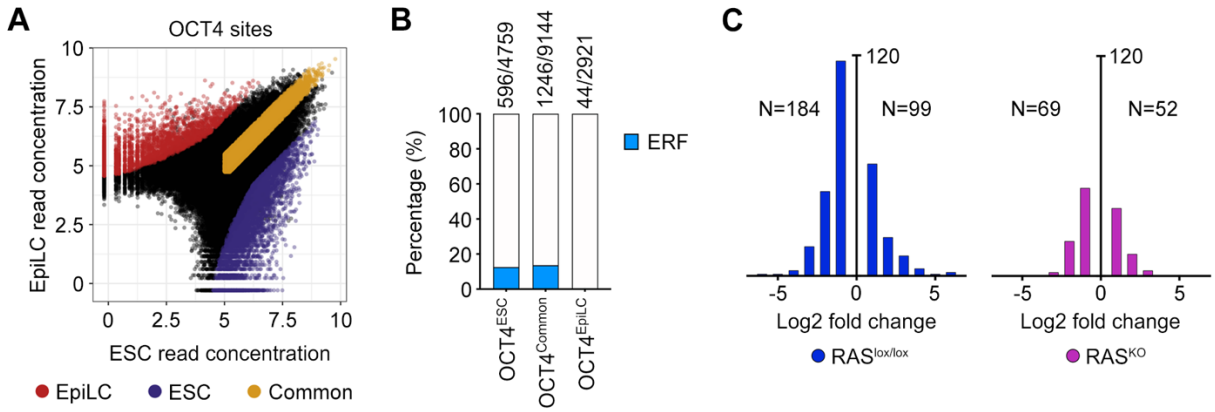


**Figure 21. Classification of OCT4/ERF co-occupied sites in ERF/OCT4$^{ESC}$, ERF/OCT4$^{EpiLC}$ or ERF/OCT4$^{Common}$. A**: Classification of OCT4 sites based on its specific enrichment during differentiation. Replicates of OCT4 peaks in ESC and EpiLC (Buecker et al., 2014) were used to determine differentially bound peaks using DiffBind (Stark and Brown, 2011). A threshold of p-val<0.01 and FDR<0.03 and >2-fold read concentration was chosen to define ESC-specific sites and EpiLC-specific sites. A set of least-changed OCT4 peaks between samples was treated as common sites. **B:** Plot showing the percentage of ERF/OCT4$^{ESC}$, ERF/OCT4$^{EpiLC}$ or ERF/OCT4$^{Common}$ referenced to the total OCT4 binding sites. **C:** Histogram plots showing fold expression changes (log2) for genes associated to ERF/OCT4$^{ESC}$ that are characterized by differential expression between ESC and EpiLC in RAS$^{lox/lox}$ and RAS$^{KO}$ cells. N indicates the total number of genes that are up or downregulated. Genes were associated at every binding site by proximity using GREAT (ref PMID: 20436461).

Since FA-RAS$^{KO}$ cells, where ERF is still highly expressed, remain trapped in an intermediate state between naïve and primed pluripotency and showed expression of naïve pluripotent markers (Figure 13), we first focused on ERF/OCT4$^{ESC}$ sites. As expected, differentially expressed genes associated with ERF/OCT4$^{ESC}$ sites were mostly downregulated during FA differentiation in RAS$^{lox/lox}$, while many of these genes did not change their expression level in RAS$^{KO}$ or those that changed showed a lower differential expression extent (Figure 21C). It has been reported that decommission of naïve enhancers by OCT4 relocation is followed by changes in enhancer chromatin patterns including decreased levels of H3K27ac (Heurtier et al., 2019). Therefore, we examined whether the naïve enhancer landscape is still fully active in FA-RAS$^{KO}$ by performing CUT&RUN analyses to evaluate the levels of H3K27ac as a marker for active enhancers and NANOG occupancy in all genotypes in 2iL conditions and after FA differentiation. Interestingly, 2iL-RAS$^{KO}$ showed increased acetylation and NANOG occupancy at ERF/OCT4$^{ESC}$ sites (Figure 22A, B). This increase in H3K27ac levels does not result in major

overall transcriptional changes and the expression level of naïve associated genes is similar between RAS$^{lox/lox}$ and RAS$^{KO}$ ESC (Figure 19C). This observation supports the idea that levels of H3K27ac does not necessarily determine enhancer activity but rather discriminates between active or poised enhancers (Zhang et al., 2020). As expected, exit from naïve pluripotency correlated with an overall decrease in H3K27ac levels, negligible chromatin-bound NANOG and reduced expression of naïve-associated genes in RAS$^{lox/lox}$ (Figure 22A, B). However, FA-RAS$^{KO}$ showed elevated gene expression, NANOG occupancy and H3K27ac levels at ERF/OCT4$^{ESC}$ sites to, in some cases, a comparable level as detected in 2iL-RAS$^{lox/lox}$ (Figure 22A, B). Together, these data showed that OCT4 binding sites associated to naïve genes remain fully active in the FA-RAS$^{KO}$ intermediate state.

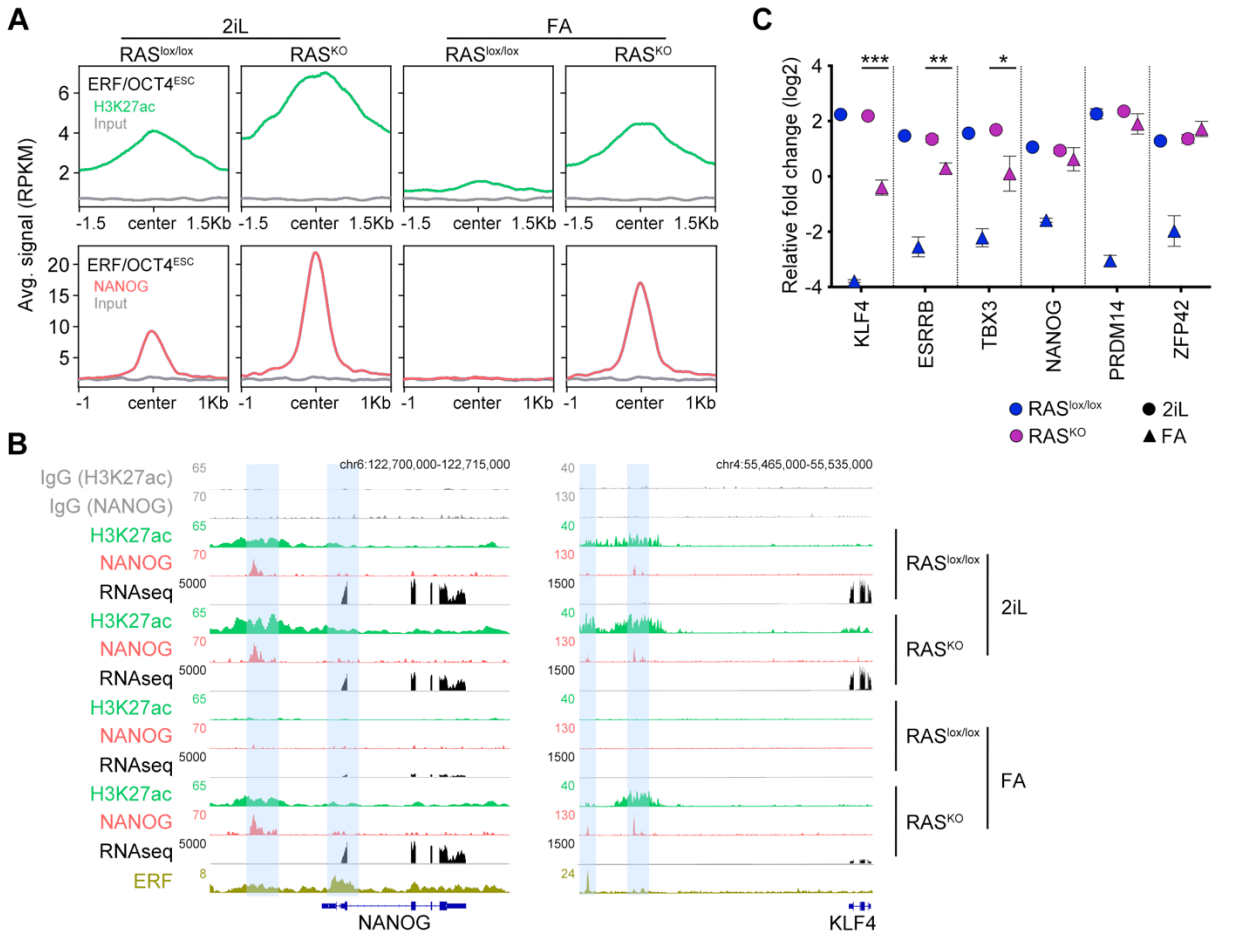


**Figure 22. The naïve enhancer landscape is active in FA-RAS$^{KO}$ ESC. A**: CUT&RUN read density plot (RPKM) showing H3K27ac (upper panel) and NANOG (lower panel) occupancy in ERF/OCT4$^{ESC}$ sites in RAS$^{lox/lox}$ and RAS$^{KO}$ cultured in 2iL or differentiated to EpiLC (FA). Corresponding inputs (IgG) are also shown as reference control. **B**: Genome browser tracks showing H3K27ac deposition, NANOG, ERF occupancy and RNA-seq RPKM read count at the KLF4 and NANOG genes in the indicated genotypes. Inputs (IgG) are also shown as a reference control. **C**: Graph showing the relative fold change (log2) expression of the indicated ERF-bound super-enhancer associated genes in RAS$^{lox/lox}$ and RAS$^{KO}$ cultured in 2iL or differentiated to EpiLC (FA). For each gene, data was normalized to the average across all samples. *** = p<0.001; ** = p<0.01; *=<0.05, t-student. Data shown are averages from triplicates and was obtained from RNA-seq datasets.

We next focused specifically on the regulatory sequences and expression level of naïve transcription factors associated with ERF-bound super-enhancers. Among these, the expression level of ERF-dependent genes (NANOG, PRDM14 and ZFP42), as defined in Figure 19A, is unaffected in FA-RAS$^{KO}$ and is comparable to 2iL-RAS$^{lox/lox}$ where ERF is still expressed (Figure 22C). However, ERF-independent genes (ESRRB, TBX3 and KLF4) showed a significant decrease in expression, suggesting that additional mechanisms ensure optimal expression of these genes in 2iL-ESC (Figure 22C). Collectively, these results demonstrated that FA-RAS$^{KO}$ retain an active naïve transcriptional network. Although some naïve markers showed a decreased expression at this stage, elevated levels of NANOG, PRDM14 or ZFP42 likely sustain the naïve like-state in FA-RAS$^{KO}$ mediated by ERF-dependent mechanisms.

## OTX2 co-occupies binding sites with NANOG in FA-RAS$^{KO}$

Global reorganization of OCT4 genomic binding during naïve to primed transition is mediated by increased expression of the transcription factor OTX2 (Buecker et al., 2014). In fact, ectopic OTX2 overexpression in 2iL-ESC is sufficient to induce OCT4 re-localization to previously inaccessible epiblast enhancer sites and, consequently, the expression of primed-associated genes (Buecker et al., 2014). It has been shown that OTX2 expression is independent of MEK signals but is efficiently repressed by the WNT pathway, explaining the elevated levels of OTX2 in the intermediate rosette pluripotent state (Neagu et al., 2020). Similarly, high levels of OTX2 have also been found to be associated to other intermediate states or formative pluripotency (Kinoshita et al., 2020, Yu et al., 2020). Interestingly, we also detected similar high OTX2 levels in FA-RAS$^{KO}$ cells compared to FA-RAS$^{lox/lox}$ (Figure 23A). Furthermore, we observed lower levels of OTX2 in 2iL-ERF$^{KO}$ ESC compared to 2iL-RAS$^{lox/lox}$ ESC (Figure 23A), suggesting that ERF might regulate the expression of OTX2. In fact, we found ERF bound to the super-enhancer region associated to OTX2 (Figure 23B). Analyzing the CUT&RUN data performed to detect enrichment for NANOG and SOX2 in RAS$^{lox/lox}$ and ERF$^{KO}$ ESC grown in 2iL conditions (described in previous sections), we observed that the decreased OTX2 expression correlated with lower NANOG and SOX2 binding. This suggests that ERF binding might prevent further OTX2 repression in the absence of FGF signaling (Figure 23B). To support these observations, we performed CUT&RUN analyses for NANOG and OTX2 in RAS$^{lox/lox}$ and RAS$^{KO}$ ESC in 2iL conditions and upon FA differentiation. In agreement, FA-RAS$^{KO}$ ESC showed strong NANOG enrichment as well as

OTX2 itself in the super-enhancer region, which could potentially sustain its own expression after NANOG is downregulated (Figure 23C).

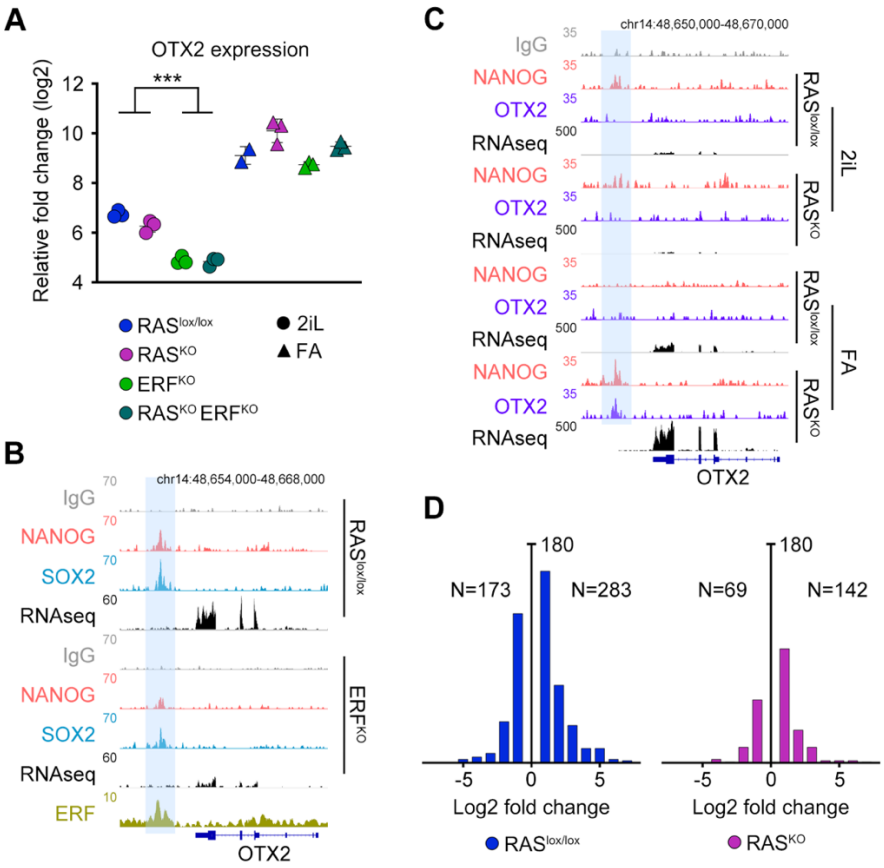


**Figure 23. OTX2 expression is regulated by ERF. A**: Plot showing the relative fold change (log2) expression for OTX2 in ESC from all genotypes cultured in 2iL or differentiated to EpiLC (FA). Data was normalized to the average across all samples. ***= p<0.001; t-student. Data shown from triplicates and was obtained from RNA-seq datasets. **B**: Genome browser tracks showing SOX2 and NANOG occupancy and RNA-seq RPKM read count at the OTX2 gene in $RAS^{lox/lox}$ and $ERF^{KO}$ ESC cultured in 2iL. ERF binding profile in $RAS^{KO}$ ESC is also shown. Inputs (IgG) are also shown as a reference control. ERF binding sites are highlighted. **C**: Genome browser tracks showing NANOG and OTX2 occupancy at the OTX2 gene and RNA-seq RPKM read count in $RAS^{lox/lox}$ and $RAS^{KO}$ ESC cultured in 2iL or differentiated to EpiLC (FA). Inputs (IgG) are also shown as a reference control. ERF binding sites are highlighted. **D**: Histogram plots showing fold expression changes (log2) for genes associated to ERF/$OCT4^{Common}$ that showed differential expression between ESC and EpiLC in $RAS^{lox/lox}$ and $RAS^{KO}$ cells. N indicates the total number of genes that are up or downregulated. Genes were associated at every binding site by proximity using GREAT (ref PMID: 20436461).

We next focused on the ERF/$OCT4^{Common}$ sites since they gained OTX2 and H3K27ac enrichment in EpiLC compared to ESC (Heurtier et al., 2019). As expected, differentially expressed genes associated with ERF/$OCT4^{Common}$ sites were mostly upregulated in FA-$RAS^{lox/lox}$ ESC (Figure 23D). Similar to what we observed with genes associated with ERF/$OCT4^{ESC}$ sites, many of these genes did not change their expression levels in FA-$RAS^{KO}$ ESC and those that changed showed a lower differential expression extent (Figure 23D). Based on the elevated levels

of NANOG expression in FA-RAS$^{KO}$ ESC, we hypothesized that ERF/OCT4$^{Common}$ sites might still retain chromatin bound NANOG. To test this idea, we analyzed the CUT&RUN data for NANOG as well as OTX2 in RAS$^{lox/lox}$ and RAS$^{KO}$ ESC in 2iL conditions and after FA differentiation. While FA-RAS$^{lox/lox}$ ESC showed negligible enrichment of NANOG, FA-RAS$^{KO}$ ESC retained NANOG bound at these sites (Figure 24A). In addition, we also observed stronger OTX2 enrichment in FA-RAS$^{KO}$ ESC compared to FA-RAS$^{lox/lox}$ ESC at these ERF/OCT4$^{Common}$ sites (Figure 24A). Interestingly, we also detected OTX2 binding in FA-RAS$^{KO}$ at the ERF/OCT4$^{ESC}$ sites, sequences associated to naïve pluripotency that are decommissioned during the transition to EpiLC (Figure 24A). Furthermore, both OTX2 and NANOG were also strongly enriched at the OCT4$^{EpiLC}$ sites in FA-RAS$^{KO}$, suggesting that, besides OCT4, OTX2 might also relocate additional naïve pluripotent factors (if expressed) to these sites prior to full differentiation (Figure 24B).

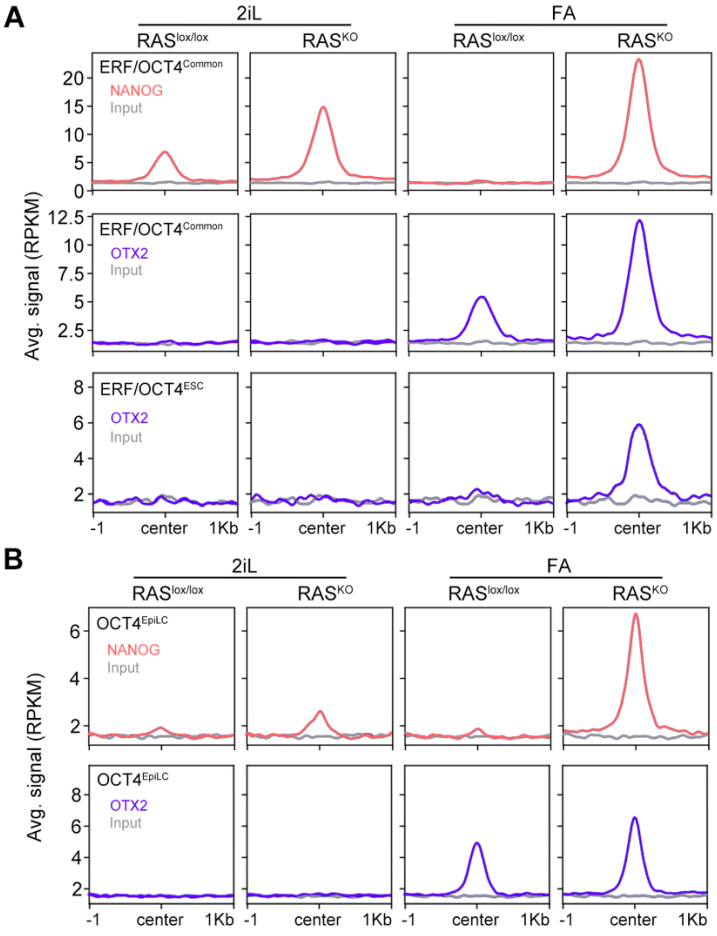


**Figure 24. OTX2 shows promiscuous binding in naïve and primed genes in FA-RAS$^{KO}$ ESC. A**: CUT&RUN read density plot (RPKM) showing NANOG and OTX2 occupancy in the indicated ERF/OCT4$^{Common}$ and ERF/OCT4$^{ESC}$ sites in RAS$^{lox/lox}$ and RAS$^{KO}$ ESC cultured in 2iL or differentiated to EpiLC (FA). Corresponding inputs (IgG) are also shown as reference control. **B**: CUT&RUN read density plot showing NANOG and OTX2 occupancy in OCT4$^{EpiLC}$ sites in RAS$^{lox/lox}$ and RAS$^{KO}$ ESC cultured in 2iL or differentiated to EpiLC (FA). Corresponding inputs (IgG) are also shown as reference control.

Lastly, we examined whether OTX2 and NANOG enrichment correlated with increased expression of post-implantation epiblast genes associated with ERF/OCT4$^{Common}$ sites in FA-RAS$^{KO}$. Interestingly, FA-RAS$^{KO}$ ESC showed similar expression levels of several primed-associated genes compared to FA-RAS$^{lox/lox}$ ESC (Figure 25). Our data demonstrated that FA-RAS$^{KO}$ ESC showed promiscuous OTX2 and NANOG binding at OCT4$^{ESC}$ and OCT4$^{EpiLC}$ sites, which correlates with the expression of both naïve and primed genes in preparation for the transition towards primed pluripotency.

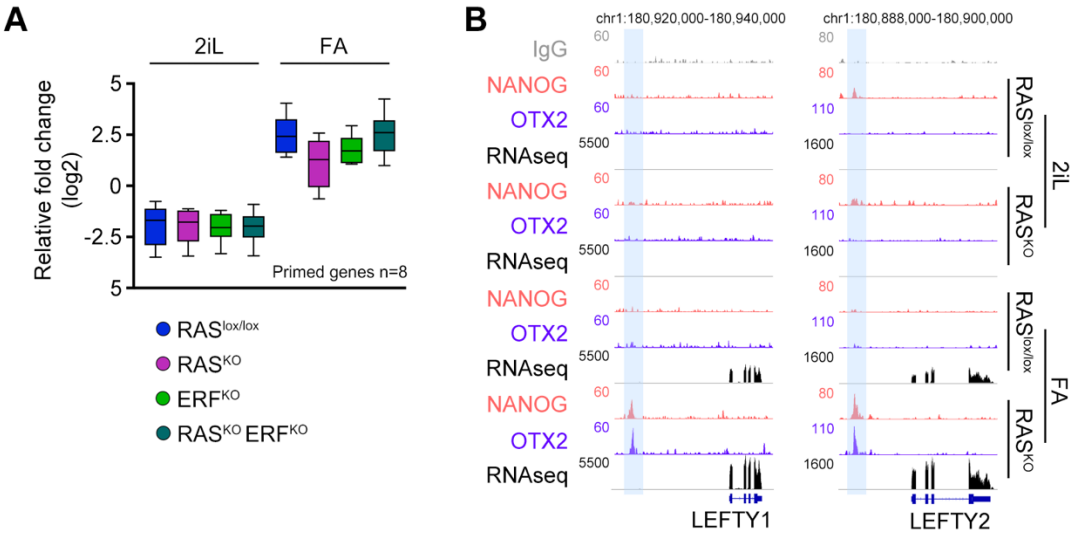


**Figure 25. OTX2 co-occupies binding sites with NANOG in FA-RAS$^{KO}$ ESC. A**: Graph showing the relative fold change (log2) expression of a subset of 8 genes associated to primed pluripotency (*Dnmt3a*, *Dnmt3b*, *Fgf5*, *Fgf15*, *OCT6*, *Wnt8a*, *Otx2* and *Dnmt3l*) in the different genotypes in 2iL or differentiated to EpiLC (FA). For each gene, data was normalized to the average across all samples and was obtained from RNA-seq datasets. **B**: Genome browser tracks showing NANOG and OTX2 occupancy and RNA-seq RPKM read count at the LEFTY1 and LEFTY2 genes in RAS$^{lox/lox}$ and RAS$^{KO}$ ESC cultured in 2iL or differentiated to EpiLC (FA). Inputs (IgG) are also shown as a reference control. ERF binding sites are highlighted.

## ERF controls the expression of LIN28 proteins

Finally, we investigated how ERF controls the exit from the developmental blockage of RAS$^{KO}$ cells by mining our RNA-seq data to identify candidate genes directly regulated by ERF. Interestingly, almost 20% of all differentially expressed genes identified in 2iL-ERF$^{KO}$ compared to 2iL-RAS$^{lox/lox}$ ESC are associated by proximity to ERF peaks and mostly overlapping ESC enhancers. Thus, by combining differential gene expression between our different genetic

conditions ($RAS^{lox/lox}$, $RAS^{KO}$, $ERF^{KO}$ and $RAS^{KO}ERF^{KO}$) and differentiation status (2iL and FA) together with nearby ERF binding occupancy, we identified LIN28A and B as putative regulators. ESC in 2iL conditions show low expression of LIN28A/B but it is upregulated by active FGF signaling during the transition to primed pluripotency. Of note, LIN28A and/or LIN28B-deficient ESC showed impaired differentiation to EpiLC, revealing a critical role for these proteins in regulating the exit from naïve pluripotency (Zhang et al., 2016). LIN28 proteins are RNA binding proteins known for binding to and inactivating the let-7 microRNA family. Functionally, let-7 microRNAs target a number of mRNA transcripts for degradation including MYC, RAS, HMGA2 and the two *de novo* methyltransferases DNMT3A and DNMT3B (Balzeau et al., 2017). Indeed, naïve ESC exhibit low levels of genome wide CpG methylation, which increase during the transition to EpiLC, correlating with the silencing of the naïve transcriptional program (Auclair et al., 2014, Takahashi et al., 2018).

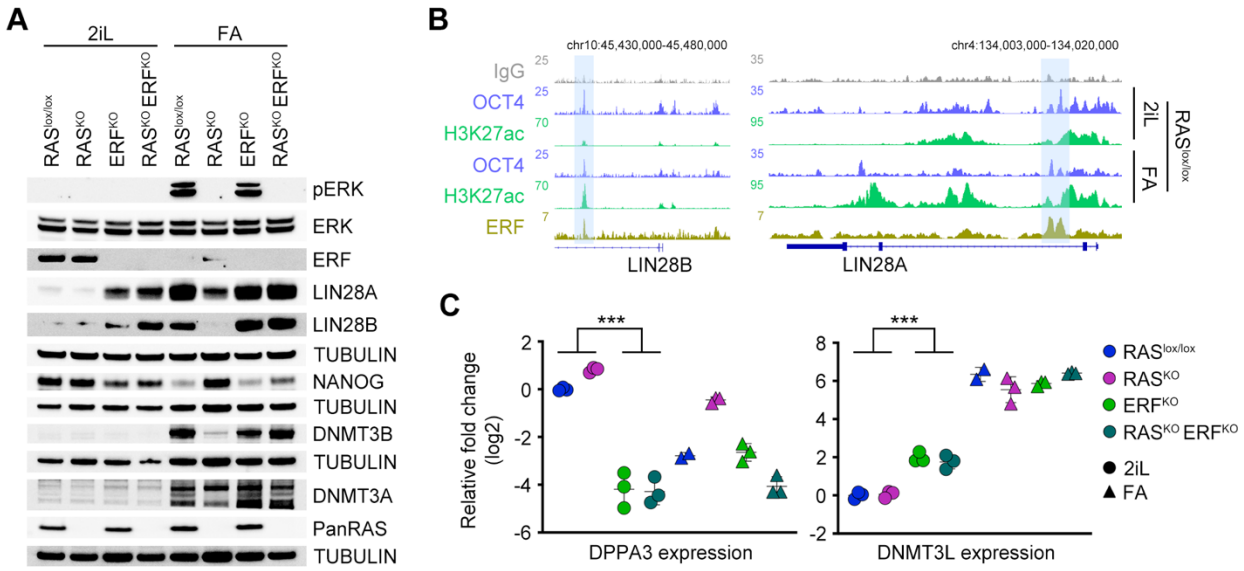


**Figure 26. ERF controls the expression of LIN28 proteins. A**: Western blot analysis of the indicated proteins performed in ESC from all genotypes cultured in 2iL or differentiated to EpiLC (FA). Tubulin levels for the corresponding blots are shown as a loading control. **B**: Genome browser tracks showing H3K27ac deposition and OCT4 occupancy at the LIN28B and LIN28A genes in $RAS^{lox/lox}$ ESC cultured in 2iL or differentiated to EpiLC (FA). ERF binding profile in $RAS^{KO}$ ESC is also shown. Inputs (IgG) are also shown as a reference control. ERF binding sites are highlighted. **C**: Plots showing the relative fold change (log2) expression for DPPA3 (left panel) and DNMT3L (right panel) in ESC from all genotypes cultured in 2iL or differentiated to EpiLC (FA). Data is shown as triplicates and was obtained from RNA-seq datasets. For each gene, data was normalized to the average across all samples. *** = p<0.001, t-student.

Based on this, we first analyzed the expression levels of LIN28 and DNMT3 proteins in our ESC. As expected, induction of EpiLC differentiation in $RAS^{lox/lox}$ and $ERF^{KO}$ showed efficient LIN28 and DNMT3 protein upregulation while FA-$RAS^{KO}$ showed low or negligible levels of LIN28 and specifically of DNMT3B (Figure 26A). Importantly, ERF deficiency restored the levels of these proteins in FA-$RAS^{KO}ERF^{KO}$ (Figure 26A). Interestingly, 2iL-$ERF^{KO}$ showed already elevated levels of LIN28 proteins before differentiation, suggesting that ERF might regulate negatively the expression of these genes. Indeed, we found that ERF binds to an enhancer region of LIN28 genes in $RAS^{KO}$ ESC (Figure 26B). Moreover, transition to EpiLC correlated with increased levels of H3K27ac at the LIN28 enhancers, and thus, LIN28 expression (Figure 26B). Of note, $ERF^{KO}$ ESC also showed low expression levels of DPPA3, implicated in preventing excessive DNA methylation in naïve pluripotency, and high expression levels of DNMT3L, the catalytically inactive regulatory factor of the DNMT3A/B (Figure 26C).

Since DNMT3 proteins are involved in the *de novo* methylation during the transition from naïve to primed pluripotency, we next examined the levels of 5-methylcytosine (5mC) by Dot blot in all different genotypes grown under naïve or primed conditions (Figure 27A). The low levels of 5mC detected in 2iL rapidly increased upon FA differentiation in $RAS^{lox/lox}$, $ERF^{KO}$ and $RAS^{KO}ERF^{KO}$ (Figure 27A). However, FA-$RAS^{KO}$ remained largely hypomethylated (Figure 27A). To further determine methylation dynamics on a genome-wide manner, we performed reduced representation bisulfite sequencing (RRBS) in all genotypes and pluripotent states (Figure 27B, C) (Meissner et al., 2005). $RAS^{lox/lox}$ in 2iL conditions presented low levels of methylation (6.55% of analyzed CpG sites are methylated), which were increased after differentiation (21.75%). Furthermore, $ERF^{KO}$ showed higher average methylation levels in 2iL (12.1%) and FA (24.7%) conditions, consistent with their bias toward differentiation and their less optimal naïve transcriptional network (Figure 27B, C). Conversely, $RAS^{KO}$ showed extremely low methylation levels in 2iL conditions (1.55%) reaching similar levels to those found in 2iL-$RAS^{lox/lox}$ when differentiated (6.9%) (Figure 27B, C). As expected, the defect in methylation observed in $RAS^{KO}$ was rescued upon ERF deletion (Figure 27B, C). Interestingly, $ERF^{KO}$ showed higher level of methylation around transcription start sites as well as in CpG islands (Figure 27D), especially after differentiation.

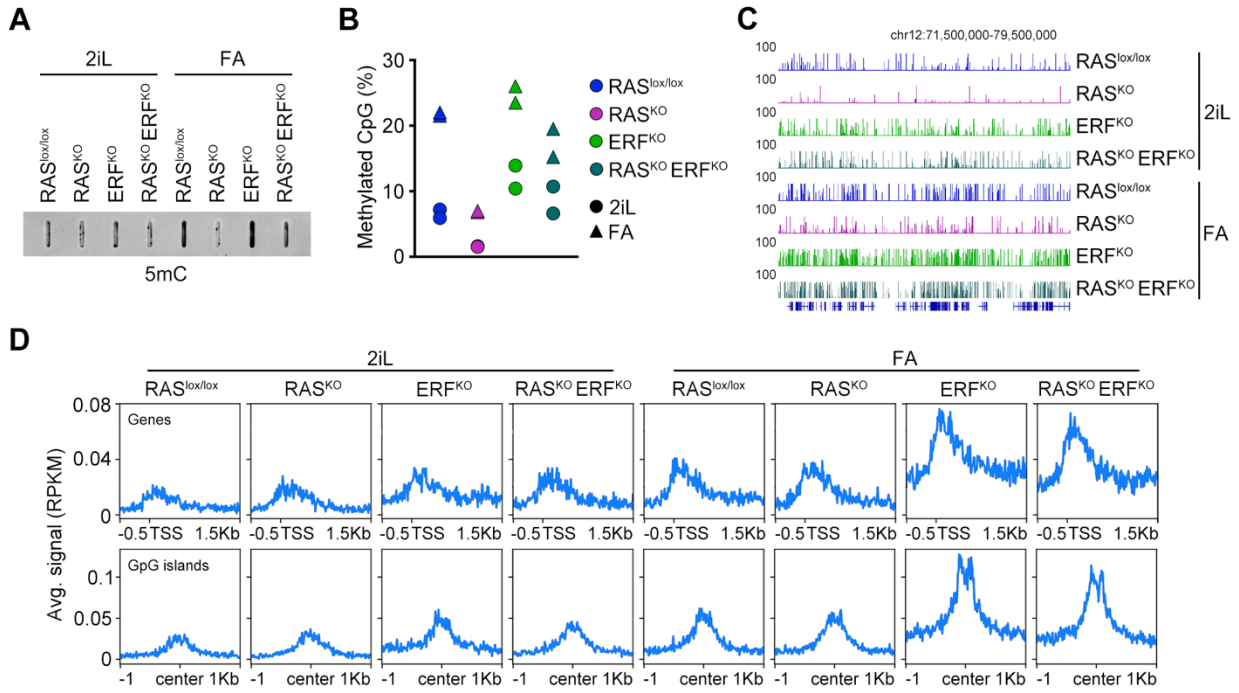


**Figure 27. ERF controls the levels of *de novo* methylation during transition to EpiLC. A**: Dot blot analysis to detect the levels of 5mC in ESC from all genotypes cultured in 2iL or differentiated to EpiLC (FA). **B**: Graph showing the percentage of methylated CpG sites identified by RRBS in ESC from all genotypes cultured in 2iL or differentiated to EpiLC (FA). **C**: Genome browser tracks showing as a representative example the level of methylation at CpG sites in a region of chromosome 12 in ESC from all genotypes cultured in 2iL or differentiated to EpiLC (FA). **D**: %CpG methylation averaged across the TSS of all protein-coding mouse genes (upper panel) or centered at CpG islands (lower panel) in ESC from all genotypes cultured in 2iL or differentiated to EpiLC (FA).

Finally, we examined whether expression of DNMT3B could rescue the developmental trapping of FA-RAS$^{KO}$ ESC. However, our results showed that DNMT3B expression is not sufficient to overcome RAS deficiency and phenocopy ERF deficiency. This suggests that decommission of naïve enhancers and super-enhancers is required in FA-RAS$^{KO}$ ESC for the transition to primed pluripotency and needs to occur prior to DNMT3B-mediated DNA methylation (Figure 28). Collectively, our data showed that ERF negatively regulates the expression of LIN28 and DNMT3 proteins and, subsequently, the altered expression of these proteins might underlie the global disbalance in the methylation levels at a genome-wide level in ERF-deficient cells.

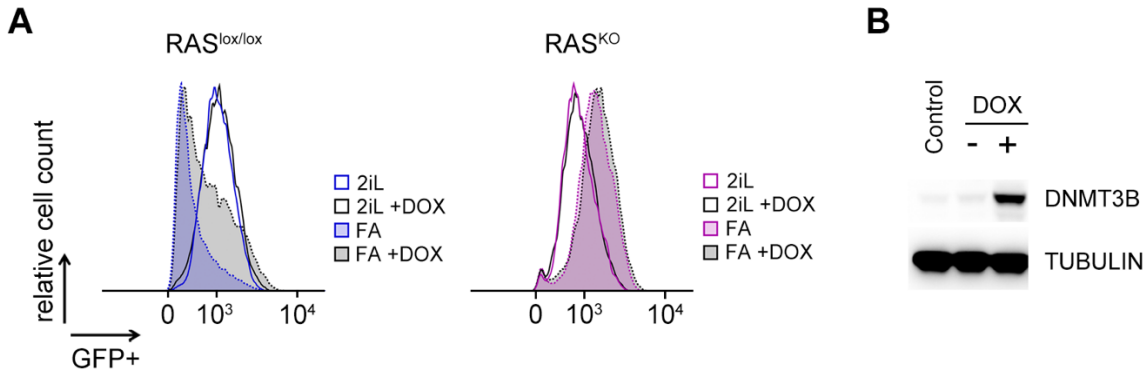


**Figure 28. The expression of DNMT3B is not sufficient to promote the progression of RAS$^{KO}$ ESC to primed pluripotency. A**: Flow cytometry analysis of REX1-deGFP reporter ESC from RAS$^{lox/lox}$ and RAS$^{KO}$ ESC cultured in 2iL or differentiated for 48 hours to EpiLC (FA). ESC were untreated or 1μg/ml DOX-treated for the duration of the experiment (48 hours) to induce DNMT3B expression. Three independent experiments were performed but one representative experiment is shown. **B**: Representative western blot analysis in RAS$^{KO}$ ESC cultured in 2iL untreated or 1μg/ml DOX-treated for 24 hours to demonstrated effective DNMT3B expression.

# DISCUSSION

The use of the pre-implantation mouse embryo as a model has provided a rich resource for studying the mechanisms underlying developmental decisions and cell fate transitions. Indeed, the implantation of the embryo into the uterus is one of the most important periods of the embryonic development. Therefore, a better understanding of how early embryonic cells restrict the developmental potential and favor cell fate specialization is needed to reveal the molecular events driving mammalian, including human, early embryo development. In addition, this knowledge has not only major clinical implications for assisted reproductive strategies such as *in vitro* fertilization (IVF) but also will help to identify new mechanisms and potential targets in diseases, such as cancer, where self-renewal and stem cell characteristics are essential.

During implantation, cells residing within the naïve ICM of the blastocyst transition through a distinct phase of primed pluripotency in preparation for lineage commitment. This transition is initiated by FGF4-dependent activation of the RAS/MAPK pathway (Kang et al., 2013, Yamanaka et al., 2010). Although this transition has been well characterized in the last few years, the downstream regulators of the signaling pathways involved in the process (FGF, WNT and TGF/BMP), remained mostly unknown. Despite the relevance of the FGF pathway and its role in promoting the exit from naïve pluripotency, little was known about how FGF signaling, and RAS proteins silence the naïve pluripotent transcriptional program and instruct this transition. In this Thesis work, we examined the molecular mechanisms coordinating the naïve to primed transition by using a RAS-deficient genetic ESC model, which allowed us to specifically dissect the role of downstream regulators of the RAS/MAPK pathway (Drosten et al., 2010, Mayor-Ruiz et al., 2018). In our previous work, we identified ERF as an important regulator downstream of the RAS pathway in ESC. Remarkably, deletion of ERF in RAS-deficient cells ($RAS^{KO}ERF^{KO}$) rescued their defects in proliferation and, more important, differentiation (Mayor-Ruiz et al., 2018). However, the molecular mechanism underlying this rescue and the precise role of ERF during early embryonic development and pluripotent transitions remained unclear.

We showed that ERF is upregulated *in vivo* during ICM formation, and it is quickly downregulated before implantation along with naïve markers (Figure 6). This is consistent with single-cell RNA-seq datasets from embryos at different developmental stages (Nowotschin et al., 2019). Moreover, RAS-deficient ESC ($RAS^{KO}$) retained elevated levels of ERF as well as naïve pluripotent markers after *in vitro* differentiation with FA (Figure 8A). These observations suggested that ERF might have a role in naïve pluripotent cells. In fact, by using different *in vitro*

models that mimic the naïve to primed pluripotent transition, we demonstrated that ERF controls the progression to primed pluripotency in a MAPK-dependent manner and its downregulation is necessary for the successful exit from naïve pluripotency (Figures 9 and 10). These results seem complementary to the requirement of ERF for trophoblast stem cells (TSC) differentiation where ERF upregulation is required to suppress the expression of FGF2 (Vorgia et al., 2017). Although FGF signaling is necessary for the self-renewal of TSC *in vitro*, ERF-dependent FGF2 transcriptional repression is necessary for proper chorionic trophoblast differentiation. Indeed, FGF2 expression is decreased in the presence of a mutant form of ERF resistant to ERK phosphorylation *in vitro* and TSC differentiation is blocked *in vivo* in ERF-knockout mice (Vorgia et al., 2017). Further studies will be necessary to reveal the precise role of ERF controlling the trophoblast transcriptional program. Nevertheless, our data revealed that the ETS transcription factor ERF is the sole FGF/MAPK-dependent switch that regulates the transition to primed pluripotency in the epiblast. The relevance of the ETS transcription factors during implantation in embryonic cells is highlighted by the role of additional ETS factors, such as ETV5, involved in promoting primed pluripotency (Kalkan et al., 2019). Nevertheless, the precise function and/or interplay between the different ETS factors differentially expressed in naïve and primed pluripotent cells is still unclear and needs further investigation.

To dissect the molecular mechanisms by which ERF is controlling this transition, we focused on characterizing the differentiated FA-RAS$^{KO}$ cells, where ERF is not downregulated and is still found in the nucleus. We showed that FA-RAS$^{KO}$ cells are characterized by an active naïve transcriptional network, high expression of OTX2 and elevated expression of both, naïve and primed markers (Figure 13). This suggests that, opposite to what has been postulated for a formative state, the activation of the primed pluripotent transcriptional program does not require a prior exit from naïve pluripotency. Indeed, formative pluripotent cells represent a transition state where none of the naïve or primed pluripotent transcriptional programs are active (Kalkan and Smith, 2014, Smith, 2017, Kinoshita and Smith, 2018). Our data also revealed that the RAS/MAPK is the main pathway controlling the exit from naïve pluripotency through the regulation of ERF levels. Indeed, we showed how ERF imposes an exquisite level of coordination during the transition from naïve to primed pluripotency. Mechanistically, ERF binds to ESC super-enhancers to ensure an optimal expression level of naïve pluripotent transcription factors, including NANOG, and protects ESC from premature commitment in the absence of RAS/MAPK signaling. In this regard, it is noteworthy that high levels of NANOG maintain the undifferentiated state of ESC in the absence of LIF and might shield naïve embryonic cells from premature commitment (Mitsui et

al., 2003, Chambers et al., 2003, Heurtier et al., 2019). Accordingly, ERF$^{KO}$ ESC showed decreased levels of NANOG and undergo a partial exit from naïve pluripotency under 2iL conditions (Figure 19). Our data suggest that ERF safeguards naïve pluripotency in the absence of MAPK signaling, at least partially, by sustaining elevated levels of NANOG, which seems sufficient to maintain an optimal naïve pluripotent state.

It seems counter-intuitive to find ERF bound to enhancers and super-enhancers controlling the expression of highly naïve transcribed genes due to the repressive nature of ERF as a transcriptional repressor (Sgouras et al., 1995, Papadaki et al., 2007). In fact, we do not have experimental support to claim that ERF is acting as a transcriptional activator, at least directly. Our current hypothesis to explain the role of ERF is based on the following: it has recently been shown that addition of CDK8/19 inhibitors (CDK8/19i) to ESC promotes the activation of enhancers and stabilizes the naïve pluripotent state as efficiently as in the 2iL conditions by facilitating Mediator activity (Lynch et al., 2020). This effect seems to be independent of the MAPK pathway since the use of CDK8/19 inhibitors eliminates the ability of the CDK8 module to repress the activity of the Mediator complex at enhancers. Accordingly, ESC grown with CDK8/19i, with an active MAPK pathway, showed phosphorylated ERF in the cytoplasm, (Martinez-Val et al., 2021) and suggests that the use of CDK8/19i can bypass the need of nuclear ERF to promote the naïve transcriptional program. Future studies will be necessary to determine whether ERF bound in active enhancers can limit the recruitment of the CDK8 module facilitating Mediator activity since MEK inhibition results in CDK8/19 inhibition (Lynch et al., 2020). In fact, other ETS transcription factors, such as ELK1, can interact directly with Mediator in a ERK phosphorylation-dependent manner (Mylona et al., 2016). Of note, the role of ERF as transcriptional repressor in silenced genes seems more canonical to its function.

Since the establishment of the culture conditions to maintain *in vitro* naïve and primed pluripotency, researchers in the field have tried to stabilize pluripotent intermediate states as it was postulated the existence of a formative pluripotent state. A state of formative pluripotency was hypothesized to be necessary to accommodate the extensive molecular reconfiguration taking place in the naïve pluripotent epiblast when transitioning to a primed state of pluripotency. This hypothesis has been recently corroborated by different groups through the identification of culture conditions to sustain formative pluripotent cells *in vitro* (Neagu et al., 2020, Kinoshita et al., 2020, Yu et al., 2020). Our work also showed that FA-RAS$^{KO}$ ESC can be maintained in culture under FAX conditions and might be a suitable model to study intermediate states of pluripotency.

In fact, FA-RAS$^{KO}$ ESC are transcriptionally similar to cells that have been differentiated with FA for 12-24 hours (Figure 14A, B). Although FA-RAS$^{KO}$ ESC are also reminiscent of the recently described intermediate states of pluripotency (Neagu et al., 2020, Kinoshita et al., 2020, Yu et al., 2020, Wang et al., 2021), there are considerable differences (Figure 14C, D). Indeed, the intermediate formative state is characterized by a silenced naïve and primed transcriptional program (Kinoshita et al., 2020, Yu et al., 2020). This is not the case for FA-RAS$^{KO}$ ESC, where the naïve transcriptional network is still active together with the expression of primed markers and thus, it might represent a unique transcriptional pluripotent state achieved by the complete absence of RAS. Our analyses revealed that RSC and FA-RAS$^{KO}$ ESC are transcriptionally more comparable, likely to the defective MAPK signaling in both intermediate states. Accordingly, similar to RSC, FAX-RAS$^{KO}$ ESC can also revert back to the initial naïve state upon restoration of the 2iL conditions, an ability that is lost in FSC (Neagu et al., 2020, Kinoshita et al., 2020). Importantly, the use of RSC demonstrated that WNT inhibition promoted rosette formation while further MEK inhibition promoted lumen formation (Neagu et al., 2020). Our results showed that RAS$^{KO}$ ESC are unable to organize a rosette even in the absence of WNT signaling (Figure 11) suggesting that RAS signaling is necessary for both rosette and lumen formation. This phenotype could have been missed using wild-type ESC, as residual MAPK activity in MEKi-treated ESC could be sufficient to facilitate rosette formation. Further work will be necessary to determine the similarity of all these intermediate states of pluripotency with their corresponding *in vivo* counterparts. Nevertheless, pluripotency can be considered as a dynamic property associated to different transient stem cell states that can be recapitulated by using different inhibitors and/or growth factors. In our case, by using RAS$^{KO}$ ESC we focused specifically on the FGF pathway and the role of RAS proteins during the naïve to primed transition.

A common feature unifies all intermediate states of pluripotency: elevated expression of the transcription factor OTX2 (Neagu et al., 2020, Kinoshita et al., 2020, Yu et al., 2020, Wang et al., 2021). Accordingly, FA-RAS$^{KO}$ ESC also showed high expression of OTX2. Importantly, OTX2 has been shown to be critical for the maintenance and self-renewal of these intermediate states (Neagu et al., 2020, Kinoshita et al., 2020, Yu et al., 2020, Wang et al., 2021). What is the precise role of OTX2 in these intermediate states of pluripotency? Earlier works have shown that over-expression of OTX2 leads to OCT4 relocation to previously inaccessible EpiLC-specific sites, downregulation of naïve pluripotent transcription factors and induction of epiblast-specific genes (Buecker et al., 2014). Remarkably, these effects occur in ESC grown with MEKi, a situation that is mimicked in FA-RAS$^{KO}$ ESC. The capacity of OTX2 to selectively engage new enhancers

depends on it levels but also on the cooperative help of other transcription factors that facilitate the access to the chromatin (Buecker et al., 2014). This ability could explain the presence of OTX2 in active naïve enhancers in FA-RAS$^{KO}$ ESC (Figure 24). In addition, we showed that, similar to OCT4, NANOG is redirected to sites that are active in EpiLC, resulting in partial or full transcriptional activation (Figure 25B). In this context, NANOG relocation might drive the recruitment of OTX2 to those sites and promote transcriptional activation. This role of NANOG promoting chromatin accessibility and the recruitment of other transcription factors together with BRG1, a member of the remodeling complex SWI/SNF, has already been shown in other studies (Heurtier et al., 2019). If NANOG has a role in promoting chromatin accessibility in EpiLC sites, it should be transient as NANOG is quickly downregulated upon exit from naïve pluripotency in wild-type ESC. By using FA-RAS$^{KO}$ ESC, which remain trapped in an intermediate state of pluripotency with high levels of NANOG, we might have captured these transient events. Whether additional naïve transcription factors (PRDM14, ESRRB, ZFP42…) are also temporarily relocated to EpiLC sites until the primed transcription factors take over on these sites will need to be addressed. However, supporting this idea is the fact that multiple naïve transcription factors are found to bind cooperatively at ESC enhancers and the enhancer shift might not only affect OCT4 or NANOG but additional naïve transcription factors. Finally, we observed that FA-RAS$^{KO}$ ESC showed heterogeneous expression levels for NANOG and OTX2 although they are both co-expressed at high levels compared to either naïve or primed RAS$^{lox/lox}$ ESC (Figure 13C, D). In fact, our data indicated that levels of NANOG are maintained during FA differentiation in RAS$^{KO}$ ESC while OTX2 levels increased dramatically in these cells. Combined, these results suggested that transition from naïve to primed pluripotency *in vitro*, more than a homogeneous and coordinated process, might be a dynamic and asynchronous progression where not all the cells respond to stimulus in the same way and at the same time.

We also showed that ERF negatively regulates the expression of LIN28 proteins as 2iL-ERF$^{KO}$ ESC showed increased levels of both LIN28A and B (Figure 26A). Although LIN28 proteins regulate the expression of DNMT3 proteins by sequestering let-7 microRNAs, we did not detect upregulation of the methyltransferases in naïve ERF$^{KO}$ ESC. This is likely due to the activity of PRDM14, which represses the expression of several genes, including DNMT3, by recruiting PRC2 (Polycomb repressive complex 2) to their promoters (Yamaji et al., 2013). Interestingly, we showed that ERF might regulate the expression of PRDM14 since it is downregulated in 2iL-ERF$^{KO}$ ESC (Figure 19A), and ERF was also found bound at its super-enhancer (Figures 19A and 20B). However, these lower levels of PRDM14 might be enough to suppress the expression of

DNMT3. Therefore, we propose that coordinated PRDM14 downregulation and increased LIN28 expression through ERF-dependent mechanisms could contribute to DNMT3 upregulation and *de novo* methylation during the transition to primed pluripotency. Of note, PRDM14 has been identified as a critical regulator during the specification of PGC from the epiblast (Yamaji et al., 2013, Yamaji et al., 2008). In addition, it has been shown that PGC-like cell (PGC-LC) induction from EpiLC can take place in the presence of MEK inhibitors (Yu et al., 2020). Combined, this suggests that ERF could play a role in germline fate specification. However, FA-RAS$^{KO}$ ESC do not have a full EpiLC phenotype and can still revert back to naïve pluripotency when transferred to 2iL conditions, which could interfere with the ability of these cells to differentiate to PGC-LC. Future work will be necessary to address whether RAS$^{KO}$ cells harbor competency for direct PGC-LC induction.

The control of ERF over LIN28 and DNMT3 proteins led us to investigate the level of methylation in all our ESC genotypes. Interestingly, ERF$^{KO}$ ESC showed increased DNA methylation compared to RAS$^{lox/lox}$ ESC and is particularly evident in genes and CpG islands after transition to EpiLC (Figure 27). Naïve ERF$^{KO}$ ESC have low levels of DNMT3 expression but elevated levels of DNMT3L (Figure 26C), the catalytically inactive regulatory factor of *de novo* DNA methyltransferases, which can contribute to this bias during differentiation (Veland et al., 2019). Furthermore, DPPA3, implicated in preventing excessive DNA methylation by sequestering the E3 ubiquitin ligase UHRF1, is also decreased in ERF$^{KO}$ ESC (Figure 26C) (Du et al., 2019). Importantly, downregulation of DPPA3 mediated by DNMT3 methylation has been shown to be a key event in the naïve to primed conversion (Sang et al., 2019). Collectively, elevated levels of DNMT3L and low levels of DPPA3 in naïve conditions could contribute to the elevated level of methylation detected in FA-ERF$^{KO}$. Nevertheless, these changes in methylation do not result in major transcriptional changes in FA-ERF$^{KO}$ compared to their respective control cells (Figure 25A). On the contrary, 2iL-RAS$^{KO}$ ESC are hypomethylated and remain in this state of low DNA methylation after FA differentiation. We hypothesized that impaired *de novo* DNA methylation could be responsible for the trapping of FA-RAS$^{KO}$ ESC in the intermediate state of pluripotency. To explore this possibility, we tested whether overexpression of DNMT3B was able to rescue the developmental block of FA-RAS$^{KO}$ ESC. However, we showed that DNMT3B expression is not sufficient to overcome RAS deficiency and promote the transition to a primed state and phenocopy ERF deficiency (Figure 28). This suggested that decommission of naïve enhancers and super-enhancers is required in FA-RAS$^{KO}$ ESC for the transition to primed pluripotency and needs to occur prior to DNMT3B-dependent DNA methylation. In agreement,

DNMT3A and DNMT3B are dispensable for a successful exit from naïve pluripotency (Li et al., 2017). However, DNMT3A/B double knockout ESC showed a retarded transition to primed pluripotency which is ultimately due to delayed CpG methylation at the proximal NANOG promoter and thus, persistent NANOG expression after 2iL withdrawal (Li et al., 2017, Farthing et al., 2008). Similarly, FA-RAS$^{KO}$ ESC showed negligible expression of DNMT3B and, therefore, high levels of NANOG and hypomethylated DNA (Figures 26A and 27).

As a corollary to our findings, we would like to speculate about the expected phenotype *in vivo* of mouse embryos lacking RAS and ERF. It has been reported that H- and N-RAS-deficient mice are viable and overall normal while K-RAS is the only member of the RAS gene family essential for embryonic development. Indeed, K-RAS-deficient mice die between E12.5 and E14.5 with fetal liver defects (Johnson et al., 1997, Koera et al., 1997). We predict that blastocysts deficient for all RAS isoforms will remain trapped in a naïve pre-implantation state. Our results suggest that loss of ERF might rescue these blastocysts *in vivo* and let them progress, at least to some extent. In fact, even if ERF deletion allows the progression and implantation of the blastocyst, it is likely that the embryo could not develop further due to the requirement of RAS and/or ERF during embryonic development (Johnson et al., 1997, Koera et al., 1997, Papadaki et al., 2007).

Finally, our studies on the role of ERF controlling pluripotency and gene expression in ESC could potentially be used to understand its role during cancer. In fact, data from the TCGA database shows that ERF is mainly found mutated in adenomas and adenocarcinomas (skin, colon or lung). Interestingly, most of these mutations generally lead to ERF loss of function suggesting that ERF behaves as a tumor suppressor. This is line with its transcriptional repressor role for well-known oncogenes such as MYC. Of note, half of all prostate cancer are caused by the TMPRSS2-ERG gene fusion, being ERG a different ETS transcription factor. This chimeric protein drives the expression of genes silenced by ERF through a competition mechanism for the same ETS binding site. In fact, loss of ERF recapitulates the features of ERG gain in prostate cells and ERF has been found recurrently being mutated in prostate cancer in an exclusive manner with the TMPRSS2-ERG gene fusion (Bose et al., 2017). Furthermore, the relevance of DNA methylation dynamics for cancer prostate formation highlights that our findings on ERF controlling methylation levels could be of relevance to determine its role in cell transformation (Massie et al., 2017).

In summary, in this Thesis work we demonstrated that ERF plays a dual role in the transition from naïve to primed pluripotency. First, ERF binds to ESC super-enhancers and regulates NANOG expression to ensure optimal expression of naïve transcription factors in the absence of FGF signaling (Figure 29). Second, activation of RAS/MAPK signaling induces the release of chromatin-bound ERF, an event that is necessary and sufficient to trigger full commitment to primed pluripotency. In addition, we also showed that ERF controls the expression of the *de novo* methyltransferase DNMT3B through LIN28 regulation, leading to the efficient inactivation of the naïve transcriptional program (Figure 29). Our data demonstrated that ERF is the MAPK-dependent switch that controls the progression to primed pluripotency in a MAPK-dependent manner.

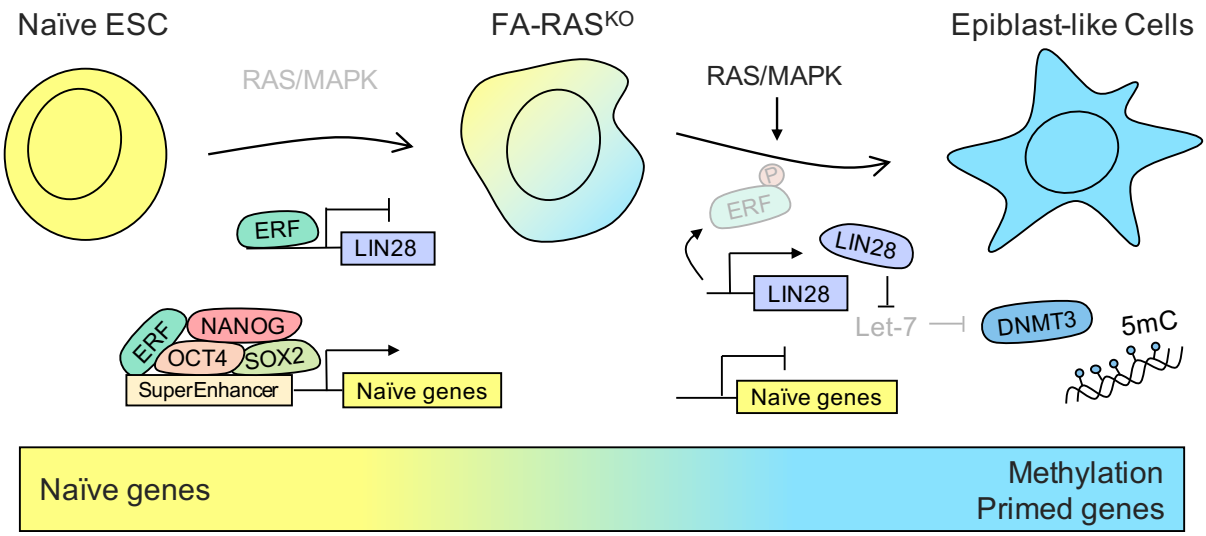


**Figure 29. Essential role of ERF as regulator in the transition to primed pluripotency in a MAPK-dependent manner.** Schematic model showing the dual role of ERF during the naïve to primed pluripotent transition. In the absence of FGF signaling, ERF ensures an optimal level of expression for naïve transcription factors. Following ERF phosphorylation and gene silencing, ESC are able to exit and transition into EpiLC associated to global CpG methylation and silencing of the naïve transcriptional network.

# CONCLUSIONS

1. ERF expression is associated to naïve pluripotency *in vivo* and *in vitro*.

2. Downregulation of ERF is necessary for the successful exit from naïve pluripotency in the absence of MAPK signaling.

3. FA-RAS$^{KO}$ ESC are trapped in an intermediate pluripotent state between naïve and primed pluripotency.

4. ERF ensures an optimal expression level of naïve pluripotent transcription factors, including NANOG, and shields ESC from premature commitment in the absence of FGF signaling.

5. The naïve enhancer landscape is active in FA-RAS$^{KO}$ ESC.

6. Upon FGF/MAPK activation, ERF is released from chromatin allowing the decommission of naïve enhancers and the full transition to primed pluripotency.

7. ERF regulates negatively the expression of *de novo* methyltransferase DNMT3B through LIN28 regulation, controlling CpG methylation during the transition to primed pluripotency.

# CONCLUSIONES

1. La expresión de ERF se asocia con el estado *naïve* de pluripotencia tanto *in vivo* como *in vitro*.

2. La eliminación de ERF es necesaria para la salida del estado *naïve* de pluripotencia en ausencia de la señalización mediada por FGF.

3. Las células madre embrionarias $RAS^{KO}$ diferenciadas se encuentran atrapadas en un estado intermedio de pluripotencia entre *naïve* y *primed*.

4. ERF garantiza un nivel de expresión óptimo de los factores de transcripción asociados a un estado de pluripotencia *naïve*, incluyendo NANOG, y protege a las ESC de diferenciar prematuramente en ausencia de FGF.

5. Los *enhancers* asociados a genes *naïve* se encuentran activos en las células madre embrionarias $RAS^{KO}$ diferenciadas.

6. En presencia de FGF, ERF se libera de la cromatina, un evento necesario y suficiente para permitir el silenciamiento de *enhancers* asociados a genes *naïve* y la transición a un estado *primed* de pluripotencia.

7. ERF controla negativamente la expresión de la metil-transferasa DNMT3B a través de LIN28, regulando la metilación en los sitios CpG durante la transición de los estados de pluripotencia *naïve* a *primed*.

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# ANNEX

## ERF peaks identified in RAS$^{KO}$ ESC

| | | |
|---|---|---|
| chr1 | 3445993 | 3446349 |
| chr1 | 3947007 | 3947285 |
| chr1 | 4611978 | 4612249 |
| chr1 | 4802556 | 4802804 |
| chr1 | 4972358 | 4972705 |
| chr1 | 5261298 | 5261554 |
| chr1 | 6059122 | 6059385 |
| chr1 | 6457934 | 6458295 |
| chr1 | 7125098 | 7125554 |
| chr1 | 7313405 | 7313735 |
| chr1 | 7671431 | 7672014 |
| chr1 | 7732745 | 7733077 |
| chr1 | 9470213 | 9470860 |
| chr1 | 9848166 | 9848567 |
| chr1 | 10852939 | 10853493 |
| chr1 | 10878282 | 10878594 |
| chr1 | 10903039 | 10903374 |
| chr1 | 11330265 | 11330547 |
| chr1 | 12022704 | 12023021 |
| chr1 | 12025865 | 12026203 |
| chr1 | 12574308 | 12574692 |
| chr1 | 12636801 | 12637090 |
| chr1 | 12744496 | 12745210 |
| chr1 | 13060049 | 13060279 |
| chr1 | 13074639 | 13075029 |
| chr1 | 13084706 | 13085389 |
| chr1 | 13104125 | 13104402 |
| chr1 | 13455606 | 13455951 |
| chr1 | 14294325 | 14294597 |
| chr1 | 14309891 | 14310133 |
| chr1 | 14312605 | 14312858 |
| chr1 | 14743046 | 14743304 |
| chr1 | 15814936 | 15815541 |
| chr1 | 16824195 | 16824493 |
| chr1 | 16824551 | 16824986 |
| chr1 | 17250854 | 17251255 |
| chr1 | 17932292 | 17932561 |
| chr1 | 18245753 | 18246148 |
| chr1 | 18639341 | 18639630 |
| chr1 | 20974821 | 20975157 |
| chr1 | 21206240 | 21206500 |
| chr1 | 21259757 | 21260424 |
| chr1 | 24092869 | 24093126 |
| chr1 | 30526643 | 30526865 |
| chr1 | 30548624 | 30548936 |
| chr1 | 30847710 | 30848010 |
| chr1 | 30937517 | 30937840 |
| chr1 | 33755822 | 33756073 |
| chr1 | 34071318 | 34071593 |
| chr1 | 34148240 | 34148575 |
| chr1 | 34842741 | 34843135 |
| chr1 | 35219406 | 35219778 |
| chr1 | 35220552 | 35221014 |
| chr1 | 35232699 | 35233020 |
| chr1 | 35238305 | 35238527 |
| chr1 | 35697571 | 35698168 |
| chr1 | 35750189 | 35750551 |
| chr1 | 36010792 | 36011173 |
| chr1 | 36013690 | 36014253 |
| chr1 | 36053885 | 36054324 |
| chr1 | 36920320 | 36920551 |
| chr1 | 36985811 | 36986241 |
| chr1 | 37210862 | 37211240 |
| chr1 | 37299547 | 37299782 |
| chr1 | 37429978 | 37430363 |
| chr1 | 38823777 | 38824275 |
| chr1 | 39528349 | 39528655 |
| chr1 | 41131434 | 41131749 |
| chr1 | 42058611 | 42058946 |
| chr1 | 42436695 | 42436938 |
| chr1 | 43484153 | 43484504 |
| chr1 | 44202534 | 44202856 |
| chr1 | 44398055 | 44398352 |
| chr1 | 45358023 | 45358311 |
| chr1 | 45795357 | 45795580 |
| chr1 | 46921650 | 46921995 |
| chr1 | 47307056 | 47307283 |
| chr1 | 47834102 | 47834414 |
| chr1 | 51400520 | 51400796 |
| chr1 | 51429723 | 51430120 |
| chr1 | 51536091 | 51536611 |
| chr1 | 51802676 | 51802898 |
| chr1 | 52009052 | 52009360 |
| chr1 | 52499959 | 52500198 |
| chr1 | 52844815 | 52845111 |
| chr1 | 52953197 | 52953778 |
| chr1 | 53823764 | 53824217 |
| chr1 | 54484670 | 54485160 |
| chr1 | 55087902 | 55088252 |
| chr1 | 55131051 | 55131340 |
| chr1 | 55131890 | 55132349 |
| chr1 | 55473806 | 55474062 |
| chr1 | 56723607 | 56724064 |
| chr1 | 56844656 | 56844887 |
| chr1 | 56952917 | 56953266 |
| chr1 | 57470306 | 57470762 |
| chr1 | 57970008 | 57970367 |
| chr1 | 58369026 | 58369271 |
| chr1 | 58392952 | 58393231 |
| chr1 | 58586381 | 58586694 |
| chr1 | 59316418 | 59316754 |
| chr1 | 59448441 | 59448910 |
| chr1 | 59472495 | 59472951 |
| chr1 | 59508357 | 59508658 |
| chr1 | 59670705 | 59670978 |
| chr1 | 59697724 | 59698187 |
| chr1 | 60426828 | 60427084 |
| chr1 | 60432316 | 60432795 |
| chr1 | 60566773 | 60567082 |
| chr1 | 60853373 | 60853780 |
| chr1 | 60857666 | 60857986 |
| chr1 | 62181592 | 62182105 |
| chr1 | 62398159 | 62398642 |
| chr1 | 62665151 | 62665442 |
| chr1 | 62701131 | 62701585 |
| chr1 | 62736454 | 62737121 |
| chr1 | 62767486 | 62767764 |
| chr1 | 63113677 | 63113914 |
| chr1 | 63138028 | 63138875 |
| chr1 | 63213932 | 63214367 |
| chr1 | 63442077 | 63442690 |
| chr1 | 63937737 | 63938062 |
| chr1 | 64122053 | 64122454 |
| chr1 | 64301368 | 64301781 |
| chr1 | 64338378 | 64338939 |
| chr1 | 65037404 | 65037921 |
| chr1 | 66960777 | 66961403 |
| chr1 | 67982997 | 67983240 |
| chr1 | 68304384 | 68304705 |
| chr1 | 71936760 | 71937038 |
| chr1 | 72242757 | 72243263 |
| chr1 | 72490315 | 72490623 |
| chr1 | 72711138 | 72711403 |
| chr1 | 73085052 | 73085286 |
| chr1 | 73523121 | 73523473 |
| chr1 | 73862558 | 73862945 |
| chr1 | 74236275 | 74236647 |
| chr1 | 74308397 | 74308690 |
| chr1 | 75027154 | 75027451 |
| chr1 | 75210702 | 75210924 |
| chr1 | 75227729 | 75227958 |
| chr1 | 75510180 | 75510476 |
| chr1 | 75521356 | 75521653 |
| chr1 | 75821266 | 75821543 |
| chr1 | 75888412 | 75889117 |
| chr1 | 76029141 | 76029587 |
| chr1 | 76036470 | 76036781 |
| chr1 | 77441491 | 77441882 |
| chr1 | 77453838 | 77454122 |
| chr1 | 77585552 | 77585827 |
| chr1 | 78119933 | 78120346 |
| chr1 | 78489091 | 78489377 |
| chr1 | 80403418 | 80403810 |
| chr1 | 81545295 | 81545531 |
| chr1 | 82476560 | 82476784 |
| chr1 | 82866811 | 82867144 |
| chr1 | 84129184 | 84129442 |
| chr1 | 84838641 | 84838911 |
| chr1 | 84839358 | 84839835 |
| chr1 | 85794241 | 85794468 |
| chr1 | 86309063 | 86309827 |
| chr1 | 86310978 | 86312056 |
| chr1 | 86348863 | 86349293 |
| chr1 | 86473089 | 86473499 |
| chr1 | 86488742 | 86489178 |
| chr1 | 86509341 | 86509754 |
| chr1 | 86511978 | 86512225 |
| chr1 | 86579847 | 86580089 |
| chr1 | 86858825 | 86859352 |
| chr1 | 87186980 | 87187271 |
| chr1 | 87213774 | 87214092 |
| chr1 | 87226568 | 87226876 |
| chr1 | 87230558 | 87230855 |
| chr1 | 87755698 | 87756104 |
| chr1 | 88277420 | 88277731 |
| chr1 | 88432567 | 88432925 |
| chr1 | 88612971 | 88613294 |
| chr1 | 88668838 | 88669244 |
| chr1 | 88924241 | 88924519 |
| chr1 | 89282598 | 89282887 |
| chr1 | 89524439 | 89524706 |
| chr1 | 89870518 | 89871164 |
| chr1 | 89939307 | 89939538 |

| | | |
|---|---|---|
| chr1 | 90527955 | 90528295 |
| chr1 | 90603272 | 90603600 |
| chr1 | 90628591 | 90629043 |
| chr1 | 91038742 | 91039070 |
| chr1 | 91250030 | 91250472 |
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| chrX | 166619150 | 166619494 |
| chrX | 167157576 | 167158076 |
| chrX | 169906098 | 169906479 |

## ERF peaks identified in RAS$^{KO}$ ESC coincident with ESC enhancers

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|---|---|---|
| chr1 | 4972358 | 4972705 |
| chr1 | 6059122 | 6059385 |
| chr1 | 6457934 | 6458295 |
| chr1 | 7313405 | 7313735 |
| chr1 | 7671431 | 7672014 |
| chr1 | 7732745 | 7733077 |
| chr1 | 10852939 | 10853493 |
| chr1 | 10878282 | 10878594 |
| chr1 | 11330265 | 11330547 |
| chr1 | 12025865 | 12026203 |
| chr1 | 12744496 | 12745210 |
| chr1 | 13060049 | 13060279 |
| chr1 | 13074639 | 13075029 |
| chr1 | 13084706 | 13085389 |
| chr1 | 13104125 | 13104402 |
| chr1 | 13455606 | 13455951 |
| chr1 | 14312605 | 14312858 |
| chr1 | 17250854 | 17251255 |
| chr1 | 18639341 | 18639630 |
| chr1 | 20974821 | 20975157 |
| chr1 | 24092869 | 24093126 |
| chr1 | 30847710 | 30848010 |
| chr1 | 35232699 | 35233020 |
| chr1 | 35697571 | 35698168 |
| chr1 | 35750189 | 35750551 |
| chr1 | 36013690 | 36014253 |
| chr1 | 36053885 | 36054324 |
| chr1 | 36985811 | 36986241 |
| chr1 | 38823777 | 38824275 |
| chr1 | 39528349 | 39528655 |
| chr1 | 42058611 | 42058946 |
| chr1 | 45358023 | 45358311 |
| chr1 | 46921650 | 46921995 |
| chr1 | 47834102 | 47834414 |
| chr1 | 51429723 | 51430120 |
| chr1 | 51536091 | 51536611 |
| chr1 | 52009052 | 52009360 |
| chr1 | 52953197 | 52953778 |
| chr1 | 54484670 | 54485160 |
| chr1 | 55131890 | 55132349 |
| chr1 | 56844656 | 56844887 |
| chr1 | 57470306 | 57470762 |
| chr1 | 59448441 | 59448910 |
| chr1 | 59472495 | 59472951 |
| chr1 | 59697724 | 59698187 |
| chr1 | 60432316 | 60432795 |
| chr1 | 60853373 | 60853780 |
| chr1 | 62181592 | 62182105 |
| chr1 | 62398159 | 62398642 |
| chr1 | 62736454 | 62737121 |
| chr1 | 62767486 | 62767764 |
| chr1 | 63138028 | 63138875 |
| chr1 | 63213932 | 63214367 |
| chr1 | 63442077 | 63442690 |
| chr1 | 63937737 | 63938062 |
| chr1 | 66960777 | 66961403 |
| chr1 | 68304384 | 68304705 |
| chr1 | 72242757 | 72243263 |
| chr1 | 74308397 | 74308690 |
| chr1 | 75027154 | 75027451 |
| chr1 | 75888412 | 75889117 |
| chr1 | 76029141 | 76029587 |
| chr1 | 76036470 | 76036781 |
| chr1 | 77441491 | 77441882 |
| chr1 | 77453838 | 77454122 |
| chr1 | 78119933 | 78120346 |
| chr1 | 80403418 | 80403810 |
| chr1 | 82866811 | 82867144 |
| chr1 | 86309063 | 86309827 |
| chr1 | 86310978 | 86312056 |
| chr1 | 86348863 | 86349293 |
| chr1 | 86488742 | 86489178 |
| chr1 | 87226568 | 87226876 |
| chr1 | 87230558 | 87230855 |
| chr1 | 88432567 | 88432925 |
| chr1 | 88612971 | 88613294 |
| chr1 | 88668838 | 88669244 |
| chr1 | 88924241 | 88924519 |
| chr1 | 89282598 | 89282887 |
| chr1 | 89870518 | 89871164 |
| chr1 | 90527955 | 90528295 |
| chr1 | 91038742 | 91039070 |
| chr1 | 100878080 | 100878591 |
| chr1 | 101757155 | 101757509 |
| chr1 | 105012647 | 105012931 |
| chr1 | 110774738 | 110775028 |
| chr1 | 118625527 | 118625749 |
| chr1 | 119048947 | 119049298 |
| chr1 | 119304931 | 119305597 |
| chr1 | 119398674 | 119399072 |
| chr1 | 120759335 | 120759887 |
| chr1 | 121123428 | 121123680 |
| chr1 | 122607452 | 122607735 |
| chr1 | 125687930 | 125688496 |
| chr1 | 127167709 | 127167974 |
| chr1 | 128392310 | 128392744 |
| chr1 | 128860189 | 128860508 |
| chr1 | 131890147 | 131890786 |
| chr1 | 132200780 | 132201210 |
| chr1 | 132281880 | 132282193 |
| chr1 | 132471101 | 132471428 |
| chr1 | 132850769 | 132851213 |
| chr1 | 132878924 | 132879318 |
| chr1 | 132981350 | 132981695 |
| chr1 | 133095455 | 133095677 |
| chr1 | 133397507 | 133398094 |
| chr1 | 133493421 | 133493728 |
| chr1 | 133694474 | 133694754 |
| chr1 | 134535002 | 134535531 |
| chr1 | 134570645 | 134570945 |
| chr1 | 135507842 | 135508140 |
| chr1 | 135675454 | 135675863 |
| chr1 | 136694915 | 136695474 |
| chr1 | 136696044 | 136696403 |
| chr1 | 137051729 | 137052025 |
| chr1 | 138956508 | 138956974 |
| chr1 | 140188576 | 140188812 |
| chr1 | 140429311 | 140429679 |
| chr1 | 143555445 | 143556025 |
| chr1 | 151878284 | 151878787 |
| chr1 | 152573271 | 152573553 |
| chr1 | 152900456 | 152900813 |
| chr1 | 152915670 | 152916190 |
| chr1 | 152942973 | 152943290 |
| chr1 | 153096157 | 153096572 |
| chr1 | 153191783 | 153192097 |
| chr1 | 153362009 | 153362404 |
| chr1 | 154080792 | 154081640 |
| chr1 | 156668610 | 156669112 |
| chr1 | 161274296 | 161274564 |
| chr1 | 164018155 | 164018550 |
| chr1 | 164377103 | 164377335 |
| chr1 | 164503472 | 164503838 |
| chr1 | 166003085 | 166003484 |
| chr1 | 166142254 | 166142533 |
| chr1 | 170871465 | 170871849 |
| chr1 | 171221503 | 171221905 |
| chr1 | 172418239 | 172418577 |
| chr1 | 176644314 | 176644718 |
| chr1 | 180570884 | 180571720 |
| chr1 | 180888685 | 180889115 |
| chr1 | 180924602 | 180925082 |
| chr1 | 182162765 | 182163476 |
| chr1 | 182181781 | 182182149 |
| chr1 | 185208512 | 185209010 |
| chr1 | 186510586 | 186510859 |
| chr1 | 186922848 | 186923232 |
| chr1 | 187724731 | 187725015 |
| chr1 | 188854302 | 188854721 |
| chr1 | 189006345 | 189006779 |
| chr1 | 189740054 | 189740456 |
| chr1 | 191065070 | 191065431 |
| chr1 | 191930673 | 191930901 |
| chr1 | 192764581 | 192764803 |
| chr10 | 4289578 | 4289881 |
| chr10 | 4375267 | 4375781 |
| chr10 | 4493064 | 4493452 |
| chr10 | 9085509 | 9085948 |
| chr10 | 9252473 | 9252808 |
| chr10 | 11229503 | 11229804 |
| chr10 | 12614319 | 12614976 |
| chr10 | 13108027 | 13108298 |
| chr10 | 15791487 | 15791725 |
| chr10 | 18469180 | 18469911 |
| chr10 | 18502068 | 18502310 |
| chr10 | 18634363 | 18634718 |
| chr10 | 19404266 | 19404707 |
| chr10 | 19835837 | 19836330 |
| chr10 | 19891771 | 19892051 |
| chr10 | 19938843 | 19939065 |
| chr10 | 20153505 | 20153748 |
| chr10 | 21102010 | 21102309 |
| chr10 | 21131005 | 21131280 |
| chr10 | 21701541 | 21702134 |
| chr10 | 21746011 | 21746506 |
| chr10 | 21829064 | 21829490 |
| chr10 | 21848076 | 21848375 |
| chr10 | 21988429 | 21988876 |
| chr10 | 22879631 | 22880177 |
| chr10 | 23806190 | 23806527 |
| chr10 | 23813183 | 23813551 |
| chr10 | 24834768 | 24834990 |
| chr10 | 25029178 | 25029886 |

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| chr10 | 26334026 | 26334407 |
| chr10 | 28087988 | 28088267 |
| chr10 | 29594975 | 29595324 |
| chr10 | 30627599 | 30627983 |
| chr10 | 34236481 | 34236759 |
| chr10 | 36623017 | 36623442 |
| chr10 | 36935895 | 36936189 |
| chr10 | 39224453 | 39224800 |
| chr10 | 39618434 | 39618661 |
| chr10 | 39975680 | 39975903 |
| chr10 | 40479866 | 40480128 |
| chr10 | 41997708 | 41998149 |
| chr10 | 43477545 | 43477879 |
| chr10 | 44408928 | 44409534 |
| chr10 | 44507984 | 44508331 |
| chr10 | 44721701 | 44721982 |
| chr10 | 45092333 | 45092707 |
| chr10 | 45446205 | 45446571 |
| chr10 | 52273909 | 52274329 |
| chr10 | 55537376 | 55537851 |
| chr10 | 56374055 | 56374756 |
| chr10 | 56406760 | 56407163 |
| chr10 | 57492162 | 57492581 |
| chr10 | 58531189 | 58531736 |
| chr10 | 59974192 | 59974722 |
| chr10 | 60606997 | 60607362 |
| chr10 | 60828236 | 60828739 |
| chr10 | 61929382 | 61929648 |
| chr10 | 62884587 | 62884895 |
| chr10 | 62892875 | 62893144 |
| chr10 | 62895512 | 62895861 |
| chr10 | 63089385 | 63089889 |
| chr10 | 63360536 | 63360861 |
| chr10 | 67083643 | 67084297 |
| chr10 | 67100122 | 67100793 |
| chr10 | 67100860 | 67101319 |
| chr10 | 67647851 | 67648113 |
| chr10 | 68137298 | 68137781 |
| chr10 | 68259455 | 68259797 |
| chr10 | 69859921 | 69860520 |
| chr10 | 69909018 | 69909413 |
| chr10 | 70325448 | 70325927 |
| chr10 | 70359877 | 70360327 |
| chr10 | 70433143 | 70433710 |
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| chr10 | 71310201 | 71310718 |
| chr10 | 71738145 | 71738580 |
| chr10 | 73896061 | 73896413 |
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| chr10 | 77193633 | 77194027 |
| chr10 | 77198984 | 77199518 |
| chr10 | 77603056 | 77603418 |
| chr10 | 78390990 | 78391532 |
| chr10 | 82383024 | 82383389 |
| chr10 | 82809466 | 82809698 |
| chr10 | 82861248 | 82861609 |
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| chr10 | 84910386 | 84910804 |
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| chr10 | 85451618 | 85452209 |
| chr10 | 85539373 | 85540131 |
| chr10 | 86434980 | 86435500 |
| chr10 | 88349790 | 88350179 |
| chr10 | 88547670 | 88547934 |
| chr10 | 90464865 | 90465316 |
| chr10 | 90709427 | 90709739 |
| chr10 | 93242027 | 93242671 |
| chr10 | 94276715 | 94277020 |
| chr10 | 95175334 | 95175809 |
| chr10 | 95220555 | 95220854 |
| chr10 | 95415468 | 95415733 |
| chr10 | 95456109 | 95456597 |
| chr10 | 95596087 | 95596352 |
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| chr10 | 95883583 | 95884193 |
| chr10 | 99265322 | 99265765 |
| chr10 | 99353467 | 99353732 |
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| chr10 | 103369012 | 103369358 |
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| chr10 | 108286867 | 108287243 |
| chr10 | 108572728 | 108573233 |
| chr10 | 109521618 | 109522143 |
| chr10 | 110931511 | 110932147 |
| chr10 | 110977383 | 110977718 |
| chr10 | 111854273 | 111854608 |
| chr10 | 112229459 | 112229751 |
| chr10 | 115469111 | 115469598 |
| chr10 | 116512600 | 116512938 |
| chr10 | 117152291 | 117152600 |
| chr10 | 117805917 | 117806353 |
| chr10 | 118461123 | 118461370 |
| chr10 | 119979995 | 119980394 |
| chr10 | 120171281 | 120171614 |
| chr10 | 120388567 | 120388920 |
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| chr10 | 121501269 | 121501665 |
| chr10 | 125725562 | 125725942 |
| chr10 | 125800514 | 125801127 |
| chr11 | 4423018 | 4423541 |
| chr11 | 4464480 | 4464943 |
| chr11 | 4803202 | 4803487 |
| chr11 | 4806193 | 4806422 |
| chr11 | 4808253 | 4808796 |
| chr11 | 6180848 | 6181247 |
| chr11 | 6778543 | 6779085 |
| chr11 | 6895111 | 6895527 |
| chr11 | 8147826 | 8148048 |
| chr11 | 8566489 | 8566826 |
| chr11 | 8569456 | 8569769 |
| chr11 | 8575420 | 8576253 |
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| chr11 | 11098157 | 11098823 |
| chr11 | 11881722 | 11881994 |
| chr11 | 11904907 | 11905287 |
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| chr11 | 12467271 | 12467656 |
| chr11 | 14159351 | 14159753 |
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| chr11 | 21988406 | 21988798 |
| chr11 | 23382750 | 23383194 |
| chr11 | 23653729 | 23654141 |
| chr11 | 23801834 | 23802243 |
| chr11 | 26103756 | 26104262 |
| chr11 | 27222285 | 27222781 |
| chr11 | 27799992 | 27800390 |
| chr11 | 28075640 | 28075886 |
| chr11 | 29597064 | 29597483 |
| chr11 | 29714301 | 29714693 |
| chr11 | 30177229 | 30177620 |
| chr11 | 30491350 | 30491761 |
| chr11 | 30750294 | 30750725 |
| chr11 | 32835099 | 32835558 |
| chr11 | 33527257 | 33527698 |
| chr11 | 34315360 | 34315949 |
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| chr11 | 34872399 | 34872682 |
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| chr11 | 39678446 | 39678887 |
| chr11 | 42109432 | 42110213 |
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| chr11 | 44767255 | 44767646 |
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| chr11 | 46059527 | 46060104 |
| chr11 | 49658969 | 49659546 |
| chr11 | 49739720 | 49740257 |
| chr11 | 52820688 | 52820972 |
| chr11 | 53202336 | 53202831 |
| chr11 | 53210862 | 53211101 |
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| chr11 | 59821532 | 59822024 |
| chr11 | 60248423 | 60248703 |
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| chr11 | 60886662 | 60887182 |
| chr11 | 61251770 | 61252177 |
| chr11 | 61529226 | 61529743 |
| chr11 | 61578093 | 61578376 |
| chr11 | 62215059 | 62215423 |
| chr11 | 62510866 | 62511306 |
| chr11 | 63350108 | 63350498 |
| chr11 | 63952544 | 63953099 |
| chr11 | 66920089 | 66920370 |
| chr11 | 67011598 | 67011974 |
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| chr11 | 68400753 | 68401118 |
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| chr11 | 69704039 | 69704315 |
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| chr11 | 71502028 | 71502662 |
| chr11 | 72576409 | 72576858 |
| chr11 | 76351318 | 76351619 |
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| chr11 | 77947854 | 77948238 |
| chr11 | 78247730 | 78248082 |
| chr11 | 78807626 | 78808105 |
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| chr11 | 79752519 | 79752834 |
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| chr11 | 80136317 | 80136728 |
| chr11 | 80889281 | 80889789 |
| chr11 | 81612913 | 81613527 |
| chr11 | 83974581 | 83974888 |
| chr11 | 84276753 | 84277226 |
| chr11 | 86701066 | 86701631 |
| chr11 | 87416049 | 87416308 |
| chr11 | 88689978 | 88690801 |
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| chr11 | 100534026 | 100534300 |
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| chr11 | 101548513 | 101549027 |
| chr11 | 101787461 | 101787688 |
| chr11 | 102331740 | 102332079 |
| chr11 | 102819276 | 102819987 |
| chr11 | 107114012 | 107114408 |
| chr11 | 107352709 | 107353015 |
| chr11 | 108269061 | 108269346 |
| chr11 | 108424028 | 108424433 |
| chr11 | 110781937 | 110782336 |
| chr11 | 111043221 | 111043721 |
| chr11 | 111843862 | 111844287 |
| chr11 | 112959579 | 112960035 |
| chr11 | 113709931 | 113710792 |
| chr11 | 114129261 | 114129781 |
| chr11 | 116387141 | 116387646 |
| chr11 | 116425016 | 116425299 |
| chr11 | 117082188 | 117082757 |
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| chr11 | 117585629 | 117586124 |
| chr11 | 117664921 | 117665673 |
| chr11 | 117975381 | 117975875 |

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| chr12 | 3738734 | 3739256 |
| chr12 | 3889837 | 3890112 |
| chr12 | 4099459 | 4099681 |
| chr12 | 4556985 | 4557471 |
| chr12 | 5067554 | 5068087 |
| chr12 | 8941884 | 8942128 |
| chr12 | 12177370 | 12177837 |
| chr12 | 12787954 | 12788227 |
| chr12 | 12938797 | 12939221 |
| chr12 | 12943076 | 12943740 |
| chr12 | 12987353 | 12987820 |
| chr12 | 14089087 | 14089377 |
| chr12 | 21462796 | 21463133 |
| chr12 | 27312113 | 27312345 |
| chr12 | 30116144 | 30116441 |
| chr12 | 31608106 | 31608441 |
| chr12 | 32824644 | 32824930 |
| chr12 | 38779302 | 38779691 |
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| chr12 | 40995653 | 40995949 |
| chr12 | 43920260 | 43920737 |
| chr12 | 48290239 | 48290519 |
| chr12 | 51858080 | 51858650 |
| chr12 | 53467500 | 53467860 |
| chr12 | 54102370 | 54102917 |
| chr12 | 55505406 | 55505808 |
| chr12 | 56284876 | 56285233 |
| chr12 | 56298429 | 56298771 |
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| chr12 | 58551309 | 58551625 |
| chr12 | 59712991 | 59713247 |
| chr12 | 65114785 | 65115344 |
| chr12 | 65428291 | 65428706 |
| chr12 | 66119401 | 66119841 |
| chr12 | 70549410 | 70549925 |
| chr12 | 70710985 | 70711407 |
| chr12 | 71030259 | 71030685 |
| chr12 | 72651241 | 72651717 |
| chr12 | 72745289 | 72745777 |
| chr12 | 72820855 | 72821327 |
| chr12 | 72853842 | 72854605 |
| chr12 | 74125953 | 74126296 |
| chr12 | 78996720 | 78997104 |
| chr12 | 80116611 | 80117307 |
| chr12 | 80217206 | 80217495 |
| chr12 | 80838743 | 80839012 |
| chr12 | 81816681 | 81817121 |
| chr12 | 81997513 | 81998019 |
| chr12 | 82402691 | 82403010 |
| chr12 | 83569926 | 83570185 |
| chr12 | 84210881 | 84211456 |
| chr12 | 84618871 | 84619322 |
| chr12 | 85753280 | 85753530 |
| chr12 | 86466110 | 86466694 |
| chr12 | 86501642 | 86502186 |
| chr12 | 86504405 | 86504874 |
| chr12 | 86802256 | 86802674 |
| chr12 | 99298853 | 99299268 |
| chr12 | 99299777 | 99300112 |
| chr12 | 100072916 | 100073177 |
| chr12 | 100337585 | 100338134 |
| chr12 | 100534100 | 100534332 |

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| chr12 | 102702298 | 102702588 |
| chr12 | 105085864 | 105086180 |
| chr12 | 105087385 | 105087800 |
| chr12 | 106175334 | 106175642 |
| chr12 | 106447053 | 106447275 |
| chr12 | 109528930 | 109529245 |
| chr12 | 110688008 | 110688324 |
| chr12 | 111321282 | 111321508 |
| chr12 | 117047854 | 117048222 |
| chr12 | 117173397 | 117173781 |
| chr12 | 117240378 | 117240662 |
| chr12 | 117684269 | 117684767 |
| chr12 | 118766469 | 118766759 |
| chr13 | 5444833 | 5445072 |
| chr13 | 6922409 | 6922703 |
| chr13 | 11005408 | 11005698 |
| chr13 | 11978907 | 11979435 |
| chr13 | 12440694 | 12441250 |
| chr13 | 13647305 | 13647608 |
| chr13 | 14170163 | 14170418 |
| chr13 | 14289986 | 14290320 |
| chr13 | 15822200 | 15822681 |
| chr13 | 18575673 | 18575977 |
| chr13 | 20935693 | 20936020 |
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| chr13 | 25052760 | 25053185 |
| chr13 | 25274991 | 25275228 |
| chr13 | 25639718 | 25640336 |
| chr13 | 28780478 | 28780874 |
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| chr5 | 140068675 | 140069049 |
| chr5 | 140174187 | 140174428 |
| chr5 | 140815109 | 140815407 |
| chr5 | 141987351 | 141987787 |
| chr5 | 142129906 | 142130479 |
| chr5 | 144479635 | 144480029 |
| chr5 | 146892942 | 146893283 |
| chr5 | 147155428 | 147155780 |
| chr5 | 148549326 | 148549709 |
| chr5 | 148550427 | 148550835 |
| chr6 | 4677434 | 4677895 |
| chr6 | 4739812 | 4740153 |
| chr6 | 5018988 | 5019783 |
| chr6 | 5033265 | 5033692 |
| chr6 | 5119226 | 5119515 |
| chr6 | 6141899 | 6142174 |
| chr6 | 7752957 | 7753467 |
| chr6 | 7823086 | 7823472 |
| chr6 | 12550226 | 12550519 |
| chr6 | 16362121 | 16362442 |
| chr6 | 18224991 | 18225365 |
| chr6 | 18485109 | 18485646 |
| chr6 | 21986030 | 21986553 |
| chr6 | 23829749 | 23829997 |
| chr6 | 25033099 | 25033632 |
| chr6 | 30028322 | 30028655 |
| chr6 | 31707294 | 31707563 |
| chr6 | 31948118 | 31948627 |
| chr6 | 34187443 | 34188076 |
| chr6 | 34344257 | 34344802 |
| chr6 | 34858768 | 34859073 |
| chr6 | 34901178 | 34901400 |
| chr6 | 35236269 | 35236590 |
| chr6 | 37688776 | 37689225 |
| chr6 | 37689721 | 37690067 |
| chr6 | 37767647 | 37767897 |
| chr6 | 37857474 | 37857920 |
| chr6 | 38357803 | 38358255 |
| chr6 | 39445869 | 39446609 |
| chr6 | 40333537 | 40333793 |
| chr6 | 42380662 | 42381317 |
| chr6 | 47602187 | 47602614 |
| chr6 | 49019367 | 49019691 |
| chr6 | 50124212 | 50124587 |
| chr6 | 50429193 | 50429734 |
| chr6 | 51708186 | 51708451 |
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| chr6 | 52105020 | 52105250 |
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| chr6 | 52822744 | 52823097 |
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| chr6 | 54849756 | 54849992 |
| chr6 | 55791872 | 55792396 |
| chr6 | 56292221 | 56292456 |
| chr6 | 59168929 | 59169225 |
| chr6 | 61430969 | 61431760 |
| chr6 | 63128948 | 63129311 |
| chr6 | 65021618 | 65022249 |
| chr6 | 65024612 | 65025084 |
| chr6 | 65270784 | 65271109 |
| chr6 | 65597047 | 65597336 |
| chr6 | 65933131 | 65933465 |
| chr6 | 67111339 | 67111931 |
| chr6 | 67236676 | 67236929 |
| chr6 | 72552746 | 72553090 |
| chr6 | 72758412 | 72758807 |
| chr6 | 72787465 | 72787728 |
| chr6 | 72794911 | 72795396 |
| chr6 | 77050795 | 77051024 |
| chr6 | 80589892 | 80590116 |
| chr6 | 81446194 | 81446758 |
| chr6 | 82174800 | 82175434 |
| chr6 | 82613187 | 82613445 |
| chr6 | 83421588 | 83422178 |
| chr6 | 85019258 | 85019538 |
| chr6 | 85286293 | 85286549 |
| chr6 | 86950930 | 86951409 |
| chr6 | 88482850 | 88483563 |
| chr6 | 91710830 | 91711144 |
| chr6 | 92247303 | 92247935 |
| chr6 | 92495298 | 92496175 |
| chr6 | 92843628 | 92843897 |
| chr6 | 93350358 | 93350711 |
| chr6 | 97048368 | 97048770 |
| chr6 | 97101650 | 97101885 |
| chr6 | 97102329 | 97102577 |
| chr6 | 98483406 | 98483897 |
| chr6 | 99615160 | 99615896 |
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| chr6 | 100180734 | 100181114 |
| chr6 | 100270581 | 100270919 |
| chr6 | 100335638 | 100336331 |
| chr6 | 100378175 | 100378544 |
| chr6 | 100419852 | 100420514 |
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| chr6 | 108070897 | 108071349 |
| chr6 | 112203099 | 112203717 |

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| chr6 | 112603854 | 112604289 |
| chr6 | 115335639 | 115335880 |
| chr6 | 116031913 | 116032195 |
| chr6 | 116057132 | 116057454 |
| chr6 | 116639670 | 116640054 |
| chr6 | 122339765 | 122340155 |
| chr6 | 122342077 | 122342521 |
| chr6 | 122591192 | 122591425 |
| chr6 | 122706989 | 122707372 |
| chr6 | 122766163 | 122766399 |
| chr6 | 124954131 | 124954789 |
| chr6 | 125502070 | 125502344 |
| chr6 | 126310960 | 126311383 |
| chr6 | 127249976 | 127250443 |
| chr6 | 127769571 | 127769810 |
| chr6 | 128142186 | 128142645 |
| chr6 | 128296464 | 128296853 |
| chr6 | 133986968 | 133987558 |
| chr6 | 134804912 | 134805184 |
| chr6 | 135040197 | 135040660 |
| chr6 | 137170175 | 137170621 |
| chr6 | 137543058 | 137543280 |
| chr6 | 137669346 | 137669691 |
| chr6 | 140336228 | 140336887 |
| chr6 | 140603089 | 140603584 |
| chr6 | 142602827 | 142603166 |
| chr6 | 142996860 | 142997154 |
| chr6 | 143099105 | 143099412 |
| chr6 | 143142237 | 143142701 |
| chr6 | 143170608 | 143171059 |
| chr6 | 144454470 | 144454715 |
| chr6 | 145275941 | 145276812 |
| chr6 | 148277250 | 148277583 |
| chr6 | 148338468 | 148338737 |
| chr6 | 148598816 | 148599495 |
| chr6 | 148992190 | 148992684 |
| chr6 | 149130893 | 149131602 |
| chr7 | 3206545 | 3206793 |
| chr7 | 3217557 | 3218056 |
| chr7 | 3347946 | 3348345 |
| chr7 | 4260736 | 4261104 |
| chr7 | 6258251 | 6258550 |
| chr7 | 6258803 | 6259444 |
| chr7 | 13014328 | 13014716 |
| chr7 | 16364979 | 16365564 |
| chr7 | 19741727 | 19742160 |
| chr7 | 19815218 | 19815597 |
| chr7 | 24505014 | 24505587 |
| chr7 | 24516989 | 24517456 |
| chr7 | 24809144 | 24809376 |
| chr7 | 24947446 | 24947758 |
| chr7 | 25263904 | 25264378 |
| chr7 | 26476772 | 26477145 |
| chr7 | 27840113 | 27840539 |
| chr7 | 28635389 | 28635754 |
| chr7 | 30265998 | 30266345 |
| chr7 | 30607762 | 30608054 |
| chr7 | 35335011 | 35335540 |
| chr7 | 35351190 | 35351680 |
| chr7 | 36602174 | 36602438 |
| chr7 | 36644236 | 36644531 |
| chr7 | 38030756 | 38031032 |
| chr7 | 43167074 | 43167662 |

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| chr7 | 43344051 | 43344449 |
| chr7 | 43608030 | 43608252 |
| chr7 | 45551634 | 45551882 |
| chr7 | 48917993 | 48918334 |
| chr7 | 52510678 | 52511132 |
| chr7 | 53136576 | 53136830 |
| chr7 | 58668680 | 58669159 |
| chr7 | 60007937 | 60008307 |
| chr7 | 62452423 | 62452734 |
| chr7 | 66158672 | 66159096 |
| chr7 | 67989380 | 67989745 |
| chr7 | 68909654 | 68909961 |
| chr7 | 70788885 | 70789311 |
| chr7 | 72326230 | 72326520 |
| chr7 | 73602650 | 73603180 |
| chr7 | 75801535 | 75801838 |
| chr7 | 78854988 | 78855498 |
| chr7 | 79139609 | 79139903 |
| chr7 | 79222796 | 79223184 |
| chr7 | 79654547 | 79655232 |
| chr7 | 80015220 | 80015760 |
| chr7 | 80199671 | 80200010 |
| chr7 | 80843976 | 80844200 |
| chr7 | 82735022 | 82735253 |
| chr7 | 83207056 | 83207466 |
| chr7 | 89997564 | 89997976 |
| chr7 | 95688157 | 95688478 |
| chr7 | 96204836 | 96205210 |
| chr7 | 96672390 | 96672939 |
| chr7 | 100699839 | 100700275 |
| chr7 | 102415894 | 102416287 |
| chr7 | 107349254 | 107349586 |
| chr7 | 107618001 | 107618517 |
| chr7 | 109381123 | 109381528 |
| chr7 | 109383274 | 109383532 |
| chr7 | 112688534 | 112688906 |
| chr7 | 112691218 | 112691684 |
| chr7 | 113142370 | 113142815 |
| chr7 | 114478930 | 114479208 |
| chr7 | 114740613 | 114740995 |
| chr7 | 115501524 | 115501795 |
| chr7 | 115866203 | 115866495 |
| chr7 | 116306656 | 116306878 |
| chr7 | 118579840 | 118580142 |
| chr7 | 118652662 | 118653014 |
| chr7 | 120695612 | 120695852 |
| chr7 | 120861114 | 120861340 |
| chr7 | 123336344 | 123336674 |
| chr7 | 124720970 | 124721434 |
| chr7 | 126377562 | 126377895 |
| chr7 | 127225200 | 127225755 |
| chr7 | 128080081 | 128080371 |
| chr7 | 130860836 | 130861216 |
| chr7 | 133114898 | 133115406 |
| chr7 | 133437748 | 133438062 |
| chr7 | 133947133 | 133947595 |
| chr7 | 134272534 | 134272999 |
| chr7 | 136430591 | 136430855 |
| chr7 | 139915617 | 139915972 |
| chr7 | 139945412 | 139945962 |
| chr7 | 139949583 | 139950265 |
| chr7 | 140959477 | 140959832 |
| chr7 | 141026353 | 141026697 |

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| chr7 | 144864479 | 144864730 |
| chr8 | 3395268 | 3395639 |
| chr8 | 4366248 | 4366650 |
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| chr8 | 4586484 | 4586976 |
| chr8 | 8984298 | 8984567 |
| chr8 | 10665881 | 10666470 |
| chr8 | 11640561 | 11641063 |
| chr8 | 12481915 | 12482152 |
| chr8 | 14014691 | 14014913 |
| chr8 | 14340037 | 14340624 |
| chr8 | 14786944 | 14787424 |
| chr8 | 15984291 | 15984828 |
| chr8 | 23561742 | 23562378 |
| chr8 | 23753941 | 23754245 |
| chr8 | 25110054 | 25110302 |
| chr8 | 25513501 | 25513764 |
| chr8 | 27240248 | 27241253 |
| chr8 | 32044106 | 32044980 |
| chr8 | 33443373 | 33444140 |
| chr8 | 33916162 | 33916543 |
| chr8 | 33993156 | 33993586 |
| chr8 | 34727765 | 34728058 |
| chr8 | 34732647 | 34733140 |
| chr8 | 34933267 | 34933502 |
| chr8 | 35268994 | 35269236 |
| chr8 | 35417678 | 35417957 |
| chr8 | 36147814 | 36148206 |
| chr8 | 36539263 | 36539639 |
| chr8 | 36547870 | 36548543 |
| chr8 | 36580995 | 36581452 |
| chr8 | 39329177 | 39329764 |
| chr8 | 40938937 | 40939491 |
| chr8 | 40962916 | 40963492 |
| chr8 | 41088618 | 41088951 |
| chr8 | 41132697 | 41133138 |
| chr8 | 43180255 | 43180630 |
| chr8 | 43320524 | 43321075 |
| chr8 | 44971315 | 44971796 |
| chr8 | 44979150 | 44979628 |
| chr8 | 46214062 | 46214385 |
| chr8 | 47690532 | 47690771 |
| chr8 | 47726826 | 47727147 |
| chr8 | 48179139 | 48179537 |
| chr8 | 48751630 | 48752377 |
| chr8 | 49194881 | 49195166 |
| chr8 | 54076225 | 54076671 |
| chr8 | 56218894 | 56219138 |
| chr8 | 56252356 | 56252649 |
| chr8 | 57732912 | 57733237 |
| chr8 | 61867055 | 61867399 |
| chr8 | 64657505 | 64657759 |
| chr8 | 65064130 | 65064542 |
| chr8 | 66323218 | 66323871 |
| chr8 | 67901301 | 67901834 |
| chr8 | 68420517 | 68420785 |
| chr8 | 69847234 | 69847582 |
| chr8 | 71526198 | 71526787 |
| chr8 | 72334327 | 72334633 |
| chr8 | 72555719 | 72556028 |
| chr8 | 74808567 | 74808995 |
| chr8 | 75014092 | 75014456 |
| chr8 | 78492985 | 78493207 |

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| chr8 | 78556663 | 78557384 |
| chr8 | 78625008 | 78625548 |
| chr8 | 79176069 | 79176452 |
| chr8 | 79804469 | 79804792 |
| chr8 | 81893297 | 81893673 |
| chr8 | 83036764 | 83037232 |
| chr8 | 83776766 | 83777329 |
| chr8 | 84539476 | 84539982 |
| chr8 | 85441643 | 85441909 |
| chr8 | 85472924 | 85473525 |
| chr8 | 85498708 | 85499113 |
| chr8 | 86393814 | 86394346 |
| chr8 | 86888061 | 86888382 |
| chr8 | 88991817 | 88992339 |
| chr8 | 89003414 | 89003841 |
| chr8 | 89015705 | 89015934 |
| chr8 | 89156899 | 89157142 |
| chr8 | 89271631 | 89271972 |
| chr8 | 90224208 | 90224439 |
| chr8 | 90851605 | 90851899 |
| chr8 | 90904340 | 90904674 |
| chr8 | 91365787 | 91366308 |
| chr8 | 92133827 | 92134414 |
| chr8 | 92303688 | 92303991 |
| chr8 | 92628987 | 92629452 |
| chr8 | 95143592 | 95144056 |
| chr8 | 98377654 | 98377955 |
| chr8 | 104410904 | 104411135 |
| chr8 | 105431996 | 105432467 |
| chr8 | 106515958 | 106516319 |
| chr8 | 107287483 | 107287928 |
| chr8 | 107595037 | 107595297 |
| chr8 | 107610967 | 107611270 |
| chr8 | 108535250 | 108535867 |
| chr8 | 108729857 | 108730381 |
| chr8 | 109462341 | 109462711 |
| chr8 | 109885212 | 109885637 |
| chr8 | 111612889 | 111613815 |
| chr8 | 111648774 | 111649335 |
| chr8 | 111789224 | 111789986 |
| chr8 | 111868704 | 111869001 |
| chr8 | 112033102 | 112033408 |
| chr8 | 114115958 | 114116365 |
| chr8 | 115010367 | 115010736 |
| chr8 | 116269493 | 116269725 |
| chr8 | 116673326 | 116673953 |
| chr8 | 117016983 | 117017237 |
| chr8 | 117342815 | 117343037 |
| chr8 | 118016143 | 118016506 |
| chr8 | 118846918 | 118847181 |
| chr8 | 119515839 | 119516117 |
| chr8 | 125460566 | 125460816 |
| chr8 | 125665919 | 125666275 |
| chr8 | 125699499 | 125699919 |
| chr8 | 127343174 | 127343518 |
| chr8 | 127884491 | 127885146 |
| chr8 | 128042944 | 128043353 |
| chr9 | 3439699 | 3439979 |
| chr9 | 7633969 | 7634481 |
| chr9 | 8462995 | 8463464 |
| chr9 | 8733507 | 8733905 |
| chr9 | 9160594 | 9161213 |
| chr9 | 14233739 | 14234273 |

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| chr9 | 15023272 | 15023555 |
| chr9 | 15317125 | 15317361 |
| chr9 | 17865548 | 17865855 |
| chr9 | 18722045 | 18722425 |
| chr9 | 18722770 | 18723014 |
| chr9 | 20978493 | 20978753 |
| chr9 | 21455300 | 21455840 |
| chr9 | 21768493 | 21768832 |
| chr9 | 22732570 | 22732905 |
| chr9 | 24818481 | 24818859 |
| chr9 | 24878350 | 24878880 |
| chr9 | 28530638 | 28530881 |
| chr9 | 28613972 | 28614393 |
| chr9 | 30597622 | 30598243 |
| chr9 | 31018715 | 31019170 |
| chr9 | 31619341 | 31619697 |
| chr9 | 31976149 | 31976517 |
| chr9 | 32095599 | 32095937 |
| chr9 | 34382170 | 34382544 |
| chr9 | 37090142 | 37090427 |
| chr9 | 37485183 | 37485577 |
| chr9 | 40783509 | 40784570 |
| chr9 | 41223443 | 41223808 |
| chr9 | 42100645 | 42101191 |
| chr9 | 45349217 | 45349573 |
| chr9 | 45349983 | 45350234 |
| chr9 | 45841271 | 45841545 |
| chr9 | 46890013 | 46890259 |
| chr9 | 48839594 | 48839887 |
| chr9 | 49023894 | 49024147 |
| chr9 | 49054176 | 49054418 |
| chr9 | 49751380 | 49751746 |
| chr9 | 53806446 | 53807034 |
| chr9 | 55101064 | 55101644 |
| chr9 | 55215827 | 55216556 |
| chr9 | 55225105 | 55225563 |
| chr9 | 55598568 | 55598886 |
| chr9 | 56072849 | 56073273 |
| chr9 | 56535414 | 56535648 |
| chr9 | 58279308 | 58279846 |
| chr9 | 59668687 | 59668961 |
| chr9 | 60787654 | 60788072 |
| chr9 | 61265360 | 61265624 |
| chr9 | 61293284 | 61293544 |
| chr9 | 61386405 | 61386722 |
| chr9 | 61667745 | 61668008 |
| chr9 | 64617507 | 64617729 |
| chr9 | 65339074 | 65339633 |
| chr9 | 65347243 | 65347591 |
| chr9 | 65641088 | 65641385 |
| chr9 | 68617301 | 68617599 |
| chr9 | 68798393 | 68798638 |
| chr9 | 70223311 | 70223584 |
| chr9 | 70257139 | 70257510 |
| chr9 | 71493859 | 71494084 |
| chr9 | 72657738 | 72658153 |
| chr9 | 73070917 | 73071500 |
| chr9 | 73094487 | 73094832 |
| chr9 | 73129595 | 73129972 |
| chr9 | 75085374 | 75085840 |
| chr9 | 77616937 | 77617340 |
| chr9 | 77777064 | 77777377 |
| chr9 | 78104217 | 78104562 |

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| chr9 | 78359675 | 78360151 |
| chr9 | 78368891 | 78369178 |
| chr9 | 79617376 | 79617696 |
| chr9 | 87755613 | 87755965 |
| chr9 | 88319201 | 88319442 |
| chr9 | 88332328 | 88332930 |
| chr9 | 88483157 | 88483537 |
| chr9 | 90834045 | 90834560 |
| chr9 | 92260929 | 92261322 |
| chr9 | 92930430 | 92930893 |
| chr9 | 94674714 | 94675062 |
| chr9 | 96603280 | 96603799 |
| chr9 | 97816392 | 97816615 |
| chr9 | 99153690 | 99154126 |
| chr9 | 101034270 | 101034512 |
| chr9 | 101041578 | 101042216 |
| chr9 | 103574234 | 103574698 |
| chr9 | 107594373 | 107594761 |
| chr9 | 108521885 | 108522166 |
| chr9 | 108723816 | 108724178 |
| chr9 | 110205985 | 110206255 |
| chr9 | 110947158 | 110947874 |
| chr9 | 111732342 | 111732625 |
| chr9 | 113192821 | 113193189 |
| chr9 | 114563989 | 114564538 |
| chr9 | 115724031 | 115724425 |
| chr9 | 117297531 | 117298179 |
| chr9 | 118266300 | 118266532 |
| chr9 | 118537908 | 118538319 |
| chr9 | 119320985 | 119321284 |
| chr9 | 119991365 | 119991828 |
| chr9 | 121989446 | 121989908 |
| chrX | 6412100 | 6412387 |
| chrX | 7764916 | 7765216 |
| chrX | 8002071 | 8002454 |
| chrX | 8207082 | 8207616 |
| chrX | 8219521 | 8220027 |
| chrX | 36775566 | 36775804 |
| chrX | 42343651 | 42343873 |
| chrX | 43467235 | 43467503 |
| chrX | 48072064 | 48072553 |
| chrX | 49125100 | 49125359 |
| chrX | 52163725 | 52164209 |
| chrX | 52189168 | 52189413 |
| chrX | 52348393 | 52348979 |
| chrX | 52753658 | 52754194 |
| chrX | 58014038 | 58014512 |
| chrX | 72328894 | 72329170 |
| chrX | 86016537 | 86016848 |
| chrX | 101084349 | 101084586 |
| chrX | 101639211 | 101639512 |
| chrX | 103472220 | 103472808 |
| chrX | 104260801 | 104261068 |
| chrX | 134261202 | 134261521 |
| chrX | 135925948 | 135926248 |
| chrX | 135973733 | 135974100 |
| chrX | 151123984 | 151124358 |
| chrX | 151792692 | 151793221 |
| chrX | 152652601 | 152653008 |
| chrX | 157601382 | 157601703 |
| chrX | 162756044 | 162756546 |
| chrX | 162832077 | 162832449 |
| chrX | 165003202 | 165003513 |

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|---|---|---|
| chrX | 166619150 | 166619494 |

## ERF peaks identified in RAS$^{KO}$ ESC coincident with ESC Super-enhancers

| | | |
|---|---|---|
| chr1 | 13060049 | 13060279 |
| chr1 | 13074639 | 13075029 |
| chr1 | 13084706 | 13085389 |
| chr1 | 13104125 | 13104402 |
| chr1 | 36013690 | 36014253 |
| chr1 | 36053885 | 36054324 |
| chr1 | 36985811 | 36986241 |
| chr1 | 89870518 | 89871164 |
| chr1 | 119304931 | 119305597 |
| chr1 | 119398674 | 119399072 |
| chr1 | 136694915 | 136695474 |
| chr1 | 136696044 | 136696403 |
| chr1 | 153096157 | 153096572 |
| chr1 | 166142254 | 166142533 |
| chr1 | 180888685 | 180889115 |
| chr1 | 180924602 | 180925082 |
| chr10 | 21102010 | 21102309 |
| chr10 | 21829064 | 21829490 |
| chr10 | 21988429 | 21988876 |
| chr10 | 59974192 | 59974722 |
| chr10 | 62884587 | 62884895 |
| chr10 | 62892875 | 62893144 |
| chr10 | 62895512 | 62895861 |
| chr10 | 67083643 | 67084297 |
| chr10 | 67100122 | 67100793 |
| chr10 | 67100860 | 67101319 |
| chr10 | 77193633 | 77194027 |
| chr10 | 77198984 | 77199518 |
| chr10 | 85539373 | 85540131 |
| chr11 | 8566489 | 8566826 |
| chr11 | 8569456 | 8569769 |
| chr11 | 8575420 | 8576253 |
| chr11 | 9116264 | 9116497 |
| chr11 | 12467271 | 12467656 |
| chr11 | 33527257 | 33527698 |
| chr11 | 62510866 | 62511306 |
| chr11 | 66920089 | 66920370 |
| chr11 | 67011598 | 67011974 |
| chr11 | 69704039 | 69704315 |
| chr11 | 97661673 | 97662609 |
| chr11 | 102331740 | 102332079 |
| chr11 | 117082188 | 117082757 |
| chr11 | 117975381 | 117975875 |
| chr12 | 12787954 | 12788227 |
| chr12 | 12938797 | 12939221 |
| chr12 | 12943076 | 12943740 |
| chr12 | 55505406 | 55505808 |
| chr12 | 56284876 | 56285233 |
| chr12 | 56298429 | 56298771 |
| chr12 | 86466110 | 86466694 |
| chr12 | 86501642 | 86502186 |
| chr12 | 86504405 | 86504874 |
| chr12 | 102702298 | 102702588 |
| chr13 | 95534273 | 95534756 |
| chr13 | 95535745 | 95535976 |
| chr13 | 97282712 | 97283384 |
| chr13 | 97454695 | 97455086 |
| chr13 | 109632795 | 109633284 |
| chr13 | 109651817 | 109652415 |
| chr14 | 21486107 | 21486610 |
| chr14 | 48654410 | 48654856 |
| chr14 | 48655130 | 48655352 |
| chr14 | 55085865 | 55086339 |
| chr14 | 63500161 | 63500716 |
| chr14 | 70635557 | 70636101 |
| chr14 | 76515587 | 76515858 |
| chr14 | 76615705 | 76616004 |
| chr14 | 99339600 | 99340069 |
| chr14 | 105851350 | 105851830 |
| chr14 | 105859020 | 105859415 |
| chr14 | 105859867 | 105860476 |
| chr14 | 105860958 | 105861325 |
| chr14 | 105897241 | 105897578 |
| chr15 | 25773625 | 25774050 |
| chr15 | 62092669 | 62093203 |
| chr15 | 88708835 | 88709250 |
| chr15 | 97396575 | 97397181 |
| chr15 | 97593658 | 97594165 |
| chr16 | 8778615 | 8779036 |
| chr16 | 23099683 | 23100259 |
| chr16 | 23102698 | 23103130 |
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| chr16 | 84772429 | 84772741 |
| chr17 | 10377643 | 10378075 |
| chr17 | 29081001 | 29081289 |
| chr17 | 31802610 | 31802832 |
| chr17 | 31806033 | 31806391 |
| chr17 | 31808118 | 31808606 |
| chr17 | 35503910 | 35504447 |
| chr17 | 35504914 | 35505267 |
| chr17 | 36997429 | 36997818 |
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| chr17 | 70900639 | 70901099 |
| chr18 | 36253776 | 36254495 |
| chr18 | 38384087 | 38384601 |
| chr18 | 38628737 | 38629230 |
| chr18 | 75344872 | 75345616 |
| chr18 | 75360594 | 75361299 |
| chr19 | 21789014 | 21789487 |
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| chr19 | 23133144 | 23133640 |
| chr19 | 53460341 | 53460591 |
| chr2 | 20654970 | 20655816 |
| chr2 | 20669479 | 20669824 |
| chr2 | 33426766 | 33427007 |
| chr2 | 152737334 | 152737860 |
| chr2 | 163051661 | 163051913 |
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| chr2 | 163062205 | 163062504 |
| chr2 | 166157355 | 166157659 |
| chr3 | 9654465 | 9655055 |
| chr3 | 34734937 | 34735351 |
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| chr3 | 34761195 | 34761438 |
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| chr3 | 96576782 | 96577061 |
| chr3 | 103207763 | 103208247 |
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| chr4 | 119071551 | 119071916 |
| chr4 | 123623412 | 123623918 |
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| chr4 | 142070587 | 142071113 |
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| chr5 | 33535563 | 33536131 |
| chr5 | 53555475 | 53555928 |
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| chr5 | 119709893 | 119710156 |
| chr5 | 119720618 | 119721273 |
| chr5 | 123134956 | 123135194 |
| chr5 | 134942781 | 134943174 |
| chr6 | 39445869 | 39446609 |
| chr6 | 65021618 | 65022249 |
| chr6 | 65024612 | 65025084 |
| chr6 | 67111339 | 67111931 |
| chr6 | 91710830 | 91711144 |
| chr6 | 122339765 | 122340155 |
| chr6 | 122342077 | 122342521 |
| chr6 | 122706989 | 122707372 |
| chr6 | 122766163 | 122766399 |
| chr6 | 143099105 | 143099412 |
| chr6 | 145275941 | 145276812 |
| chr7 | 3206545 | 3206793 |
| chr7 | 3217557 | 3218056 |
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| chr7 | 45551634 | 45551882 |
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| chr7 | 80199671 | 80200010 |
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| chr8 | 33916162 | 33916543 |
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| chr8 | 85472924 | 85473525 |
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| chr8 | 89003414 | 89003841 |
| chr8 | 89015705 | 89015934 |
| chr9 | 56535414 | 56535648 |
| chr9 | 58279308 | 58279846 |
| chr9 | 78359675 | 78360151 |
| chr9 | 78368891 | 78369178 |
| chr9 | 110947158 | 110947874 |
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| chrX | 8002071 | 8002454 |
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| chr1 | 13649937 | 13650437 |
| chr1 | 13664264 | 13664764 |
| chr1 | 14189570 | 14190070 |
| chr1 | 14421026 | 14421526 |
| chr1 | 14613170 | 14613670 |
| chr1 | 14743018 | 14743518 |
| chr1 | 16631308 | 16631808 |
| chr1 | 16651333 | 16651833 |
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| chr1 | 35841620 | 35842120 |
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| chr1 | 38823854 | 38824354 |
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| chr1 | 39456525 | 39457025 |
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| chr1 | 39528285 | 39528785 |
| chr1 | 39865126 | 39865626 |
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| chr1 | 42724872 | 42725372 |
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| chr1 | 51906462 | 51906962 |
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| chr1 | 52127338 | 52127838 |
| chr1 | 52656550 | 52657050 |
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| chr1 | 55215334 | 55215834 |
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| chr1 | 55575784 | 55576284 |
| chr1 | 55966202 | 55966702 |
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| chr1 | 57470284 | 57470784 |
| chr1 | 57612132 | 57613112 |
| chr1 | 58400631 | 58401131 |
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| chr1 | 59924403 | 59924903 |
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| chr1 | 89878369 | 89878869 |
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| chr1 | 93275489 | 93275989 |
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| chr1 | 127783750 | 127784250 |
| chr1 | 127997167 | 127997667 |
| chr1 | 130710531 | 130711031 |
| chr1 | 131145877 | 131146377 |
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| chr1 | 132158690 | 132159190 |
| chr1 | 132277080 | 132277580 |
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| chr1 | 133146564 | 133147064 |
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| chr1 | 136138973 | 136139473 |
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| chr9 | 99415729 | 99416229 |
| chr9 | 99419852 | 99420352 |
| chr9 | 99437925 | 99438425 |
| chr9 | 101041671 | 101042171 |
| chr9 | 102148329 | 102148829 |
| chr9 | 102528003 | 102528503 |
| chr9 | 102719860 | 102720360 |
| chr9 | 102794274 | 102794774 |
| chr9 | 103000260 | 103000760 |

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| chr9 | 103138838 | 103139338 |
| chr9 | 103504514 | 103505014 |
| chr9 | 103508530 | 103509030 |
| chr9 | 103751541 | 103752041 |
| chr9 | 103907331 | 103907831 |
| chr9 | 104065703 | 104066696 |
| chr9 | 104361577 | 104362077 |
| chr9 | 104922016 | 104922516 |
| chr9 | 105599185 | 105599685 |
| chr9 | 105907349 | 105907849 |
| chr9 | 105971492 | 105971992 |
| chr9 | 106166621 | 106167121 |
| chr9 | 106171822 | 106172322 |
| chr9 | 106485213 | 106485713 |
| chr9 | 107349627 | 107350127 |
| chr9 | 107575476 | 107575976 |
| chr9 | 108144181 | 108144681 |
| chr9 | 108287855 | 108288355 |
| chr9 | 108521768 | 108522268 |
| chr9 | 108654635 | 108655135 |
| chr9 | 108753118 | 108753618 |
| chr9 | 108849764 | 108850264 |
| chr9 | 109909796 | 109910296 |
| chr9 | 110051103 | 110051603 |
| chr9 | 110400713 | 110401213 |
| chr9 | 110488755 | 110489255 |
| chr9 | 110951383 | 110951883 |
| chr9 | 110952826 | 110953326 |
| chr9 | 111147344 | 111147844 |
| chr9 | 111226487 | 111226987 |
| chr9 | 111243808 | 111244308 |
| chr9 | 111486502 | 111487002 |
| chr9 | 111732289 | 111732789 |
| chr9 | 113649114 | 113649614 |
| chr9 | 114394098 | 114394598 |
| chr9 | 114395242 | 114395742 |
| chr9 | 114564760 | 114565260 |
| chr9 | 114778776 | 114779276 |
| chr9 | 114780662 | 114781162 |
| chr9 | 115030469 | 115030969 |
| chr9 | 115034738 | 115035238 |
| chr9 | 115107413 | 115107913 |
| chr9 | 115169382 | 115169882 |
| chr9 | 115711440 | 115711940 |
| chr9 | 116032571 | 116033071 |
| chr9 | 116145335 | 116145835 |
| chr9 | 116213168 | 116213668 |
| chr9 | 116316708 | 116317208 |
| chr9 | 116423115 | 116423615 |
| chr9 | 116427339 | 116427839 |
| chr9 | 116464550 | 116465050 |
| chr9 | 116468880 | 116469380 |
| chr9 | 116500931 | 116501431 |
| chr9 | 116639898 | 116640398 |
| chr9 | 118266256 | 118266756 |
| chr9 | 118608586 | 118609086 |
| chr9 | 118943823 | 118944323 |
| chr9 | 118995457 | 118995957 |
| chr9 | 119271472 | 119271972 |
| chr9 | 119958747 | 119959247 |
| chr9 | 120116212 | 120116712 |
| chr9 | 120149404 | 120149904 |
| chr9 | 120152238 | 120152738 |
| chr9 | 121317021 | 121317521 |
| chr9 | 121335565 | 121336065 |
| chr9 | 121614221 | 121614721 |
| chr9 | 123456854 | 123457354 |
| chr_rDNA | 8406 | 8906 |
| chr_rDNA | 10231 | 10731 |
| chrX | 6753431 | 6753931 |
| chrX | 7659199 | 7659699 |
| chrX | 8001967 | 8002467 |
| chrX | 8008489 | 8008989 |
| chrX | 12543504 | 12544004 |
| chrX | 13057727 | 13058227 |
| chrX | 47970973 | 47971473 |
| chrX | 48062823 | 48063323 |
| chrX | 48064073 | 48064573 |
| chrX | 48459283 | 48459783 |
| chrX | 48893872 | 48894372 |
| chrX | 49250712 | 49251212 |
| chrX | 52183885 | 52184385 |
| chrX | 56467592 | 56468092 |
| chrX | 58016265 | 58016765 |
| chrX | 60187646 | 60188146 |
| chrX | 70712917 | 70713417 |
| chrX | 71218788 | 71219288 |
| chrX | 72328777 | 72329277 |
| chrX | 73560672 | 73561172 |
| chrX | 73739166 | 73739666 |
| chrX | 79606459 | 79606959 |
| chrX | 93097460 | 93097960 |
| chrX | 93663826 | 93664326 |
| chrX | 99017472 | 99017972 |
| chrX | 99028455 | 99028955 |
| chrX | 99608183 | 99608683 |
| chrX | 101481493 | 101481993 |
| chrX | 101864707 | 101865207 |
| chrX | 104364577 | 104365077 |
| chrX | 113180823 | 113181323 |
| chrX | 129332867 | 129333367 |
| chrX | 130547909 | 130548409 |
| chrX | 140094024 | 140094524 |
| chrX | 140460382 | 140460882 |
| chrX | 142157975 | 142158475 |
| chrX | 144328022 | 144328522 |
| chrX | 150400341 | 150400841 |
| chrX | 151792762 | 151793262 |
| chrX | 157446673 | 157447173 |
| chrX | 157448924 | 157449424 |
| chrX | 157815393 | 157815893 |
| chrX | 159943502 | 159944002 |
| chrX | 160448344 | 160448844 |
| chrX | 162885126 | 162885626 |
| chrX | 163203351 | 163203851 |

## OCT4 peaks identified specifically in EpiLC

| chr1 | 3549504 | 3550004 |
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| chr1 | 4139102 | 4139602 |
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| chr1 | 5227856 | 5228356 |
| chr1 | 5655548 | 5656048 |
| chr1 | 6898196 | 6898696 |
| chr1 | 7967883 | 7968383 |
| chr1 | 8557808 | 8558308 |
| chr1 | 8915264 | 8915764 |
| chr1 | 11013039 | 11013539 |
| chr1 | 11416320 | 11416820 |
| chr1 | 11423707 | 11424207 |
| chr1 | 12751272 | 12751772 |
| chr1 | 12814572 | 12815072 |
| chr1 | 12835146 | 12835646 |
| chr1 | 13496320 | 13496820 |
| chr1 | 13620209 | 13620709 |
| chr1 | 13622015 | 13622515 |
| chr1 | 14934572 | 14935072 |
| chr1 | 15355185 | 15355685 |
| chr1 | 15483786 | 15484286 |
| chr1 | 16188121 | 16188621 |
| chr1 | 16293806 | 16294306 |
| chr1 | 17009559 | 17010059 |
| chr1 | 17506643 | 17507143 |
| chr1 | 18831002 | 18831502 |
| chr1 | 20980433 | 20980933 |
| chr1 | 22293874 | 22294374 |
| chr1 | 23538421 | 23538921 |
| chr1 | 24050601 | 24051101 |
| chr1 | 25310004 | 25310504 |
| chr1 | 26388446 | 26388946 |
| chr1 | 34386605 | 34387105 |
| chr1 | 34468439 | 34468939 |
| chr1 | 36042411 | 36042911 |
| chr1 | 36593026 | 36593526 |
| chr1 | 38618370 | 38618870 |
| chr1 | 38795423 | 38795923 |
| chr1 | 38869302 | 38869802 |
| chr1 | 41783514 | 41784014 |
| chr1 | 42654631 | 42655131 |
| chr1 | 44998305 | 44998805 |
| chr1 | 45883362 | 45883862 |
| chr1 | 45926007 | 45926507 |
| chr1 | 45994433 | 45994933 |
| chr1 | 46152862 | 46153362 |
| chr1 | 46858348 | 46858848 |
| chr1 | 47102943 | 47103443 |
| chr1 | 47914156 | 47914656 |
| chr1 | 48488517 | 48489017 |
| chr1 | 51271788 | 51272288 |
| chr1 | 51548820 | 51549320 |
| chr1 | 51704017 | 51704517 |
| chr1 | 53191241 | 53191741 |
| chr1 | 53613113 | 53613613 |
| chr1 | 53866350 | 53866850 |
| chr1 | 55731266 | 55731766 |
| chr1 | 57857966 | 57858466 |
| chr1 | 57890080 | 57890580 |
| chr1 | 58190876 | 58191376 |
| chr1 | 58889787 | 58890287 |

| chr1 | 61480623 | 61481123 |
|---|---|---|
| chr1 | 61481682 | 61482182 |
| chr1 | 64087461 | 64087961 |
| chr1 | 64207101 | 64207601 |
| chr1 | 64247739 | 64248239 |
| chr1 | 64298904 | 64299404 |
| chr1 | 64303111 | 64303611 |
| chr1 | 64311367 | 64311867 |
| chr1 | 65306771 | 65307271 |
| chr1 | 65440103 | 65440603 |
| chr1 | 65666260 | 65666760 |
| chr1 | 65684338 | 65684838 |
| chr1 | 66442797 | 66443297 |
| chr1 | 69355306 | 69355806 |
| chr1 | 69466675 | 69467175 |
| chr1 | 70789807 | 70790307 |
| chr1 | 70806667 | 70807167 |
| chr1 | 72797204 | 72797704 |
| chr1 | 72813885 | 72814385 |
| chr1 | 73744442 | 73744942 |
| chr1 | 75616717 | 75617217 |
| chr1 | 77634639 | 77635139 |
| chr1 | 78140393 | 78141272 |
| chr1 | 78181815 | 78182315 |
| chr1 | 78228636 | 78229136 |
| chr1 | 78388759 | 78389259 |
| chr1 | 78567351 | 78567851 |
| chr1 | 81718194 | 81718694 |
| chr1 | 83101734 | 83102234 |
| chr1 | 83542009 | 83542509 |
| chr1 | 84217664 | 84218164 |
| chr1 | 85740887 | 85741387 |
| chr1 | 85756130 | 85756630 |
| chr1 | 87313072 | 87313572 |
| chr1 | 88192059 | 88192559 |
| chr1 | 88577505 | 88578005 |
| chr1 | 88583621 | 88584121 |
| chr1 | 88608167 | 88608667 |
| chr1 | 88609732 | 88610232 |
| chr1 | 88957103 | 88957603 |
| chr1 | 88995859 | 88996359 |
| chr1 | 90353360 | 90353860 |
| chr1 | 90729059 | 90729559 |
| chr1 | 90733801 | 90734301 |
| chr1 | 91083010 | 91083510 |
| chr1 | 91088298 | 91088798 |
| chr1 | 97863102 | 97863602 |
| chr1 | 97996990 | 97997490 |
| chr1 | 99661003 | 99661503 |
| chr1 | 99907738 | 99908238 |
| chr1 | 99970694 | 99971194 |
| chr1 | 100416668 | 100417168 |
| chr1 | 100446261 | 100446761 |
| chr1 | 100806510 | 100807010 |
| chr1 | 105002430 | 105002930 |
| chr1 | 106629401 | 106629901 |
| chr1 | 106721971 | 106722471 |
| chr1 | 108181348 | 108182253 |
| chr1 | 109981920 | 109982420 |
| chr1 | 112643210 | 112643710 |
| chr1 | 114641198 | 114641698 |

| chr1 | 115843613 | 115844113 |
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| chr1 | 115926258 | 115926758 |
| chr1 | 115931055 | 115931555 |
| chr1 | 115932004 | 115932504 |
| chr1 | 116070156 | 116070656 |
| chr1 | 116276572 | 116277396 |
| chr1 | 119470664 | 119471164 |
| chr1 | 119485836 | 119486336 |
| chr1 | 120204798 | 120205298 |
| chr1 | 120696114 | 120696614 |
| chr1 | 120961795 | 120962295 |
| chr1 | 122667193 | 122667693 |
| chr1 | 123322785 | 123323285 |
| chr1 | 125272620 | 125273120 |
| chr1 | 127143366 | 127143866 |
| chr1 | 127238901 | 127239401 |
| chr1 | 127262137 | 127262637 |
| chr1 | 127263004 | 127263504 |
| chr1 | 127328442 | 127328942 |
| chr1 | 127575506 | 127576006 |
| chr1 | 127697609 | 127698109 |
| chr1 | 129134376 | 129134876 |
| chr1 | 131086420 | 131086920 |
| chr1 | 131427440 | 131427940 |
| chr1 | 131946374 | 131946874 |
| chr1 | 132659531 | 132660031 |
| chr1 | 132747812 | 132748312 |
| chr1 | 132815025 | 132815525 |
| chr1 | 136571503 | 136572003 |
| chr1 | 136665008 | 136665508 |
| chr1 | 138154000 | 138154500 |
| chr1 | 138371794 | 138372294 |
| chr1 | 139657594 | 139658094 |
| chr1 | 139692529 | 139693029 |
| chr1 | 140065811 | 140066311 |
| chr1 | 140066454 | 140066954 |
| chr1 | 140379535 | 140380035 |
| chr1 | 140912642 | 140913142 |
| chr1 | 141454859 | 141455359 |
| chr1 | 142108823 | 142109323 |
| chr1 | 143820368 | 143820868 |
| chr1 | 144896856 | 144897356 |
| chr1 | 147215654 | 147216154 |
| chr1 | 149430826 | 149431326 |
| chr1 | 151778617 | 151779117 |
| chr1 | 154157384 | 154157884 |
| chr1 | 155086340 | 155086840 |
| chr1 | 155113890 | 155114390 |
| chr1 | 156474725 | 156475225 |
| chr1 | 156476088 | 156476588 |
| chr1 | 156611783 | 156612283 |
| chr1 | 156663140 | 156663640 |
| chr1 | 157069202 | 157069702 |
| chr1 | 157449877 | 157450377 |
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| chr1 | 159535486 | 159535986 |
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| chr1 | 161463679 | 161464179 |
| chr1 | 162607596 | 162608096 |

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| chr1 | 164008009 | 164008509 |
| chr1 | 164128297 | 164128797 |
| chr1 | 165770783 | 165771283 |
| chr1 | 167065947 | 167066447 |
| chr1 | 168334842 | 168335342 |
| chr1 | 168550008 | 168550508 |
| chr1 | 170499723 | 170500223 |
| chr1 | 170793358 | 170793858 |
| chr1 | 171301268 | 171301768 |
| chr1 | 174963973 | 174964473 |
| chr1 | 176037615 | 176038115 |
| chr1 | 176071869 | 176072369 |
| chr1 | 177693701 | 177694201 |
| chr1 | 178496179 | 178496679 |
| chr1 | 180497554 | 180498054 |
| chr1 | 181290876 | 181291376 |
| chr1 | 181340798 | 181341298 |
| chr1 | 181839509 | 181840009 |
| chr1 | 182686240 | 182686740 |
| chr1 | 185098243 | 185098743 |
| chr1 | 185928811 | 185929311 |
| chr1 | 187432241 | 187432741 |
| chr1 | 187907821 | 187908321 |
| chr1 | 188055874 | 188056374 |
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| chr1 | 191494987 | 191495487 |
| chr1 | 191515450 | 191516398 |
| chr1 | 191524719 | 191525219 |
| chr1 | 191698360 | 191698860 |
| chr1 | 192647787 | 192648287 |
| chr1 | 192796404 | 192796904 |
| chr1 | 192814636 | 192815136 |
| chr1 | 193672419 | 193672919 |
| chr10 | 3851927 | 3852427 |
| chr10 | 5444858 | 5445358 |
| chr10 | 5677814 | 5678314 |
| chr10 | 7232766 | 7233266 |
| chr10 | 7234026 | 7234526 |
| chr10 | 7234864 | 7235364 |
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| chr10 | 10998612 | 10999112 |
| chr10 | 12909121 | 12909621 |
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| chr10 | 17831022 | 17831522 |
| chr10 | 18827687 | 18828187 |
| chr10 | 19998639 | 19999139 |
| chr10 | 20178635 | 20179135 |
| chr10 | 20298489 | 20298989 |
| chr10 | 21128372 | 21128872 |
| chr10 | 21251976 | 21252476 |
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| chr10 | 22155048 | 22155548 |
| chr10 | 22698389 | 22698889 |
| chr10 | 23195260 | 23195760 |
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| chr10 | 25887169 | 25887669 |
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| chr10 | 26827473 | 26827973 |
| chr10 | 26876185 | 26876685 |
| chr10 | 27313631 | 27314131 |
| chr10 | 28541429 | 28541929 |
| chr10 | 28649652 | 28650152 |
| chr10 | 28815124 | 28815624 |
| chr10 | 29365324 | 29365824 |
| chr10 | 31615280 | 31615780 |
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| chr10 | 33945573 | 33946073 |
| chr10 | 35645789 | 35646289 |
| chr10 | 37552355 | 37552855 |
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| chr10 | 40809461 | 40809961 |
| chr10 | 41182556 | 41183056 |
| chr10 | 43170968 | 43171468 |
| chr10 | 43188171 | 43188671 |
| chr10 | 43481066 | 43481566 |
| chr10 | 43651438 | 43651938 |
| chr10 | 44074844 | 44075344 |
| chr10 | 44478259 | 44478759 |
| chr10 | 44549424 | 44549924 |
| chr10 | 44810770 | 44811270 |
| chr10 | 45943576 | 45944076 |
| chr10 | 46605889 | 46606389 |
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| chr10 | 49018112 | 49018612 |
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| chr10 | 51615118 | 51615618 |
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| chr10 | 57489708 | 57490208 |
| chr10 | 57562504 | 57563004 |
| chr10 | 58355815 | 58356315 |
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| chr10 | 67791548 | 67792048 |
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| chr10 | 70357856 | 70358356 |
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| chr10 | 73092123 | 73092623 |
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| chr10 | 75943981 | 75944481 |
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| chr10 | 84110251 | 84110751 |
| chr10 | 84363739 | 84364239 |
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| chr10 | 89518766 | 89519266 |
| chr10 | 90019126 | 90019626 |
| chr10 | 90804567 | 90805067 |
| chr10 | 92112669 | 92113169 |
| chr10 | 94525282 | 94525782 |
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| chr10 | 103225474 | 103225974 |
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| chr10 | 105110056 | 105110556 |
| chr10 | 106115537 | 106116037 |
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| chr10 | 115005486 | 115005986 |
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| chr10 | 117452127 | 117452627 |
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| chr10 | 117848149 | 117848649 |
| chr10 | 118711079 | 118711908 |
| chr10 | 119065454 | 119065954 |
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| chr10 | 119859458 | 119859958 |
| chr10 | 121447670 | 121448170 |
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| chr10 | 122931845 | 122932345 |
| chr10 | 123061500 | 123062000 |
| chr10 | 123671227 | 123671727 |
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| chr10 | 123807204 | 123807704 |
| chr10 | 124320079 | 124320579 |
| chr10 | 124400329 | 124400829 |
| chr10 | 126531833 | 126532333 |
| chr10 | 127112583 | 127113083 |
| chr10 | 128111261 | 128111761 |
| chr10 | 128424725 | 128425225 |
| chr10 | 128534495 | 128534995 |
| chr10 | 130281735 | 130282235 |
| chr11 | 3147369 | 3147869 |
| chr11 | 3148302 | 3148802 |
| chr11 | 3177273 | 3177773 |
| chr11 | 3545748 | 3546248 |
| chr11 | 3794565 | 3795065 |
| chr11 | 4012498 | 4012998 |
| chr11 | 5129084 | 5129584 |
| chr11 | 5164472 | 5164972 |
| chr11 | 5562918 | 5563418 |
| chr11 | 6178699 | 6179199 |
| chr11 | 6364527 | 6365027 |
| chr11 | 6684705 | 6685205 |
| chr11 | 6923871 | 6924371 |
| chr11 | 7182617 | 7183117 |
| chr11 | 7281618 | 7282118 |
| chr11 | 7282852 | 7283352 |
| chr11 | 7943498 | 7943998 |
| chr11 | 8051545 | 8052045 |
| chr11 | 9237089 | 9237589 |
| chr11 | 9874090 | 9874590 |
| chr11 | 9904239 | 9904739 |
| chr11 | 10046596 | 10047096 |
| chr11 | 10296661 | 10297161 |
| chr11 | 10612251 | 10612751 |
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| chr7 | 139966816 | 139967316 |
| chr7 | 140348206 | 140348706 |
| chr7 | 140625302 | 140625802 |
| chr7 | 140974616 | 140975116 |
| chr7 | 140975355 | 140975855 |
| chr7 | 142830909 | 142831409 |
| chr7 | 142948598 | 142949098 |
| chr7 | 143879687 | 143880187 |
| chr7 | 143954014 | 143954514 |
| chr7 | 144232180 | 144232680 |
| chr7 | 144898497 | 144898997 |
| chr8 | 6607128 | 6607628 |
| chr8 | 6608712 | 6609212 |
| chr8 | 8279577 | 8280077 |
| chr8 | 8609136 | 8609636 |
| chr8 | 8616241 | 8616741 |
| chr8 | 8619556 | 8620056 |
| chr8 | 8655044 | 8655544 |
| chr8 | 10871401 | 10871901 |
| chr8 | 10925519 | 10926019 |
| chr8 | 10971940 | 10972440 |
| chr8 | 11460394 | 11460894 |
| chr8 | 13948404 | 13948904 |
| chr8 | 16172236 | 16172736 |
| chr8 | 16314378 | 16314878 |
| chr8 | 17354236 | 17354736 |
| chr8 | 17654156 | 17654656 |
| chr8 | 18023599 | 18024099 |
| chr8 | 25392665 | 25393165 |
| chr8 | 25437073 | 25437573 |
| chr8 | 28346389 | 28346889 |
| chr8 | 28383317 | 28383817 |
| chr8 | 28630688 | 28631188 |
| chr8 | 28702902 | 28703402 |
| chr8 | 30604912 | 30605412 |
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| chr8 | 33606189 | 33606689 |
| chr8 | 34689934 | 34690434 |

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| chr8 | 34703519 | 34704019 |
| chr8 | 34781804 | 34782304 |
| chr8 | 34987997 | 34988497 |
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| chr8 | 35212690 | 35213190 |
| chr8 | 35703643 | 35704143 |
| chr8 | 36472953 | 36473453 |
| chr8 | 42958362 | 42958862 |
| chr8 | 43407299 | 43407799 |
| chr8 | 43879854 | 43880354 |
| chr8 | 45614547 | 45615047 |
| chr8 | 45658612 | 45659112 |
| chr8 | 46005221 | 46005721 |
| chr8 | 46010183 | 46010683 |
| chr8 | 46833736 | 46834236 |
| chr8 | 46940143 | 46940643 |
| chr8 | 47135570 | 47136070 |
| chr8 | 47482289 | 47482789 |
| chr8 | 49508810 | 49509310 |
| chr8 | 60567024 | 60567524 |
| chr8 | 60567964 | 60568464 |
| chr8 | 60570271 | 60570771 |
| chr8 | 60571078 | 60571578 |
| chr8 | 60574887 | 60575387 |
| chr8 | 60938991 | 60939491 |
| chr8 | 61417063 | 61417563 |
| chr8 | 61927803 | 61928303 |
| chr8 | 62235262 | 62235762 |
| chr8 | 66473245 | 66473745 |
| chr8 | 66869503 | 66870003 |
| chr8 | 68493997 | 68494497 |
| chr8 | 68558320 | 68558820 |
| chr8 | 73400402 | 73400902 |
| chr8 | 74295783 | 74296283 |
| chr8 | 75244390 | 75244890 |
| chr8 | 75636989 | 75637489 |
| chr8 | 75640242 | 75640742 |
| chr8 | 76016562 | 76017062 |
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| chr8 | 79078148 | 79078648 |
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| chr8 | 79615610 | 79616110 |
| chr8 | 81419833 | 81420333 |
| chr8 | 82742891 | 82743391 |
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| chr8 | 84239579 | 84240079 |
| chr8 | 85893776 | 85894276 |
| chr8 | 86550470 | 86550970 |
| chr8 | 87152346 | 87152846 |
| chr8 | 87210507 | 87211007 |
| chr8 | 87265005 | 87265505 |
| chr8 | 88437661 | 88438161 |
| chr8 | 89242383 | 89242883 |
| chr8 | 89926680 | 89927180 |
| chr8 | 90244695 | 90245195 |
| chr8 | 90854416 | 90854916 |
| chr8 | 90897047 | 90897547 |
| chr8 | 91509740 | 91510240 |
| chr8 | 92070515 | 92071015 |
| chr8 | 92181218 | 92181718 |
| chr8 | 92216234 | 92216734 |
| chr8 | 92222953 | 92223453 |
| chr8 | 92301558 | 92302058 |

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| chr8 | 92302630 | 92303130 |
| chr8 | 92314506 | 92315006 |
| chr8 | 93626794 | 93627294 |
| chr8 | 97389751 | 97390251 |
| chr8 | 102862949 | 102863449 |
| chr8 | 103145558 | 103146058 |
| chr8 | 104212799 | 104213299 |
| chr8 | 104375022 | 104375522 |
| chr8 | 104806092 | 104806592 |
| chr8 | 105937940 | 105938440 |
| chr8 | 106159416 | 106159916 |
| chr8 | 106558827 | 106559327 |
| chr8 | 106610900 | 106611400 |
| chr8 | 107777012 | 107777512 |
| chr8 | 107818867 | 107819367 |
| chr8 | 107820107 | 107820607 |
| chr8 | 109137304 | 109137804 |
| chr8 | 109516265 | 109516765 |
| chr8 | 113405293 | 113405793 |
| chr8 | 115038341 | 115038841 |
| chr8 | 117071191 | 117071691 |
| chr8 | 117251044 | 117251544 |
| chr8 | 117508453 | 117508953 |
| chr8 | 118485044 | 118485544 |
| chr8 | 118888281 | 118888781 |
| chr8 | 119844463 | 119844963 |
| chr8 | 119845272 | 119845772 |
| chr8 | 120666862 | 120667362 |
| chr8 | 122814441 | 122814941 |
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| chr8 | 124805938 | 124806438 |
| chr8 | 125218236 | 125218736 |
| chr8 | 125412963 | 125413463 |
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| chr8 | 126967772 | 126968272 |
| chr8 | 128173408 | 128173908 |
| chr8 | 128496380 | 128496880 |
| chr9 | 4117229 | 4117729 |
| chr9 | 6286752 | 6287252 |
| chr9 | 7719962 | 7720462 |
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| chr9 | 7900382 | 7900882 |
| chr9 | 7960239 | 7960739 |
| chr9 | 8459020 | 8459520 |
| chr9 | 9043298 | 9043798 |
| chr9 | 10637185 | 10637685 |
| chr9 | 10713654 | 10714154 |
| chr9 | 12381237 | 12381737 |
| chr9 | 12930170 | 12930670 |
| chr9 | 12937291 | 12937791 |
| chr9 | 13690405 | 13690905 |
| chr9 | 14059109 | 14059609 |
| chr9 | 14116969 | 14117469 |
| chr9 | 14246259 | 14246759 |
| chr9 | 15437423 | 15437923 |
| chr9 | 17681596 | 17682096 |
| chr9 | 17816843 | 17817343 |
| chr9 | 17862019 | 17862519 |
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| chr9 | 18467299 | 18467799 |
| chr9 | 18685932 | 18686432 |

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| chr9 | 18697809 | 18698309 |
| chr9 | 20552132 | 20552632 |
| chr9 | 21983855 | 21984355 |
| chr9 | 23204195 | 23204695 |
| chr9 | 25185652 | 25186152 |
| chr9 | 27556465 | 27556965 |
| chr9 | 29307070 | 29307570 |
| chr9 | 30155763 | 30156263 |
| chr9 | 30308186 | 30308686 |
| chr9 | 30573155 | 30573655 |
| chr9 | 30765940 | 30766440 |
| chr9 | 31376672 | 31377172 |
| chr9 | 31380569 | 31381069 |
| chr9 | 32215635 | 32216135 |
| chr9 | 32607033 | 32607533 |
| chr9 | 32882020 | 32882520 |
| chr9 | 33233796 | 33234296 |
| chr9 | 38033114 | 38033614 |
| chr9 | 40614001 | 40614501 |
| chr9 | 42042364 | 42042864 |
| chr9 | 42652092 | 42652592 |
| chr9 | 42985038 | 42985538 |
| chr9 | 44232977 | 44233477 |
| chr9 | 45042954 | 45043454 |
| chr9 | 45840572 | 45841072 |
| chr9 | 46660124 | 46660624 |
| chr9 | 46967229 | 46967729 |
| chr9 | 46981997 | 46982497 |
| chr9 | 47485240 | 47485740 |
| chr9 | 48208353 | 48208853 |
| chr9 | 48240298 | 48240798 |
| chr9 | 48632807 | 48633307 |
| chr9 | 48987418 | 48987918 |
| chr9 | 49571973 | 49572473 |
| chr9 | 49879655 | 49880155 |
| chr9 | 49935965 | 49936465 |
| chr9 | 50268725 | 50269225 |
| chr9 | 50554535 | 50555035 |
| chr9 | 50884623 | 50885123 |
| chr9 | 51434552 | 51435052 |
| chr9 | 54566941 | 54567441 |
| chr9 | 55122571 | 55123071 |
| chr9 | 56531936 | 56532436 |
| chr9 | 56609436 | 56609936 |
| chr9 | 57273387 | 57273887 |
| chr9 | 57392998 | 57393498 |
| chr9 | 59245456 | 59245956 |
| chr9 | 59316286 | 59316786 |
| chr9 | 63069190 | 63069690 |
| chr9 | 63073975 | 63074475 |
| chr9 | 63499777 | 63500277 |
| chr9 | 63980391 | 63980891 |
| chr9 | 64455774 | 64456274 |
| chr9 | 64612328 | 64612828 |
| chr9 | 64615770 | 64616270 |
| chr9 | 64649776 | 64650276 |
| chr9 | 65211617 | 65212117 |
| chr9 | 65625004 | 65625504 |
| chr9 | 65689615 | 65690115 |
| chr9 | 65848112 | 65848612 |
| chr9 | 65875441 | 65875941 |
| chr9 | 66597778 | 66598278 |
| chr9 | 66863937 | 66864437 |

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| chr9 | 67510893 | 67511393 |
| chr9 | 68991378 | 68991878 |
| chr9 | 69668623 | 69669123 |
| chr9 | 70182560 | 70183060 |
| chr9 | 70260450 | 70260950 |
| chr9 | 72135682 | 72136182 |
| chr9 | 72273529 | 72274029 |
| chr9 | 72814511 | 72815011 |
| chr9 | 75959769 | 75960269 |
| chr9 | 76355848 | 76356348 |
| chr9 | 76695507 | 76696007 |
| chr9 | 77427651 | 77428151 |
| chr9 | 80504456 | 80504956 |
| chr9 | 81019976 | 81020476 |
| chr9 | 82807181 | 82807681 |
| chr9 | 82970398 | 82970898 |
| chr9 | 83400285 | 83400785 |
| chr9 | 83434420 | 83434920 |
| chr9 | 83628749 | 83629249 |
| chr9 | 83707085 | 83707585 |
| chr9 | 84375708 | 84376208 |
| chr9 | 84754377 | 84754877 |
| chr9 | 85282876 | 85283376 |
| chr9 | 85651904 | 85652404 |
| chr9 | 86390423 | 86390923 |
| chr9 | 86668581 | 86669081 |
| chr9 | 87147929 | 87148429 |
| chr9 | 90903538 | 90904038 |
| chr9 | 91667018 | 91667518 |
| chr9 | 91953102 | 91953602 |
| chr9 | 92515820 | 92516320 |
| chr9 | 93297248 | 93297748 |
| chr9 | 95121085 | 95121585 |
| chr9 | 96027814 | 96028314 |
| chr9 | 96731062 | 96731562 |
| chr9 | 96892475 | 96892975 |
| chr9 | 98722566 | 98723066 |
| chr9 | 98725247 | 98725747 |
| chr9 | 98727440 | 98727940 |
| chr9 | 98750930 | 98751430 |
| chr9 | 98753268 | 98753768 |
| chr9 | 99258793 | 99259293 |
| chr9 | 100312204 | 100312704 |
| chr9 | 102211387 | 102211887 |
| chr9 | 103860977 | 103861477 |
| chr9 | 104101423 | 104101923 |
| chr9 | 104194387 | 104194887 |
| chr9 | 104255596 | 104256096 |
| chr9 | 104346640 | 104347140 |
| chr9 | 105284355 | 105284855 |
| chr9 | 105537437 | 105537937 |
| chr9 | 105976867 | 105977367 |
| chr9 | 106450518 | 106451018 |
| chr9 | 107305493 | 107305993 |
| chr9 | 107975349 | 107975849 |
| chr9 | 108273688 | 108274188 |
| chr9 | 109201556 | 109202056 |
| chr9 | 109526062 | 109526562 |
| chr9 | 109547771 | 109548271 |
| chr9 | 109674598 | 109675098 |
| chr9 | 110949147 | 110949647 |
| chr9 | 112054580 | 112055080 |
| chr9 | 112071089 | 112071589 |

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|---|---|---|
| chr9 | 113615587 | 113616087 |
| chr9 | 117290250 | 117290750 |
| chr9 | 118818353 | 118818853 |
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| chr9 | 122614746 | 122615246 |
| chr9 | 122821147 | 122821647 |
| chr9 | 123135099 | 123135599 |
| chr9 | 123347944 | 123348444 |
| chr9 | 123355684 | 123356184 |
| chr9 | 124408582 | 124409082 |
| chrX | 6942816 | 6943316 |
| chrX | 6964283 | 6964783 |
| chrX | 7868474 | 7868974 |
| chrX | 12119363 | 12119863 |
| chrX | 12766735 | 12767235 |
| chrX | 13233255 | 13233755 |
| chrX | 13297293 | 13297793 |
| chrX | 19408809 | 19409309 |
| chrX | 19701676 | 19702176 |
| chrX | 22833128 | 22833628 |
| chrX | 22961325 | 22961825 |
| chrX | 36411629 | 36412129 |
| chrX | 38491811 | 38492311 |
| chrX | 43032772 | 43033272 |
| chrX | 45152550 | 45153050 |
| chrX | 45854507 | 45855007 |
| chrX | 46092235 | 46092735 |
| chrX | 47618387 | 47618887 |
| chrX | 50450879 | 50451379 |
| chrX | 50456080 | 50456580 |
| chrX | 50968451 | 50968951 |
| chrX | 51897010 | 51897510 |
| chrX | 57855692 | 57856192 |
| chrX | 57917656 | 57918156 |
| chrX | 57974552 | 57975052 |
| chrX | 60718369 | 60718869 |
| chrX | 60719764 | 60720264 |
| chrX | 60788374 | 60788874 |
| chrX | 62698118 | 62698618 |
| chrX | 64955726 | 64956226 |
| chrX | 66678608 | 66679108 |
| chrX | 71412680 | 71413180 |
| chrX | 71537133 | 71537633 |
| chrX | 72634512 | 72635012 |
| chrX | 75882674 | 75883174 |
| chrX | 77426202 | 77426702 |
| chrX | 82741473 | 82741973 |
| chrX | 82893009 | 82893509 |
| chrX | 95155811 | 95156311 |
| chrX | 95487408 | 95487908 |
| chrX | 98252605 | 98253105 |
| chrX | 100802047 | 100802547 |
| chrX | 101089354 | 101089854 |
| chrX | 101140694 | 101141194 |
| chrX | 102571102 | 102571602 |
| chrX | 103636631 | 103637131 |
| chrX | 103646426 | 103646926 |
| chrX | 103648121 | 103648621 |
| chrX | 103652999 | 103653499 |
| chrX | 103922280 | 103922780 |
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| chrX | 111631104 | 111631604 |
| chrX | 114965792 | 114966292 |
| chrX | 118557464 | 118557964 |
| chrX | 118596092 | 118596592 |
| chrX | 127058210 | 127058710 |
| chrX | 128576417 | 128576917 |
| chrX | 128577310 | 128577810 |
| chrX | 134158179 | 134158679 |
| chrX | 134163158 | 134163658 |
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| chrX | 138676108 | 138676608 |
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| chrX | 144314925 | 144315425 |
| chrX | 146669571 | 146670071 |
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| chrX | 152815657 | 152816157 |
| chrX | 156841157 | 156841657 |
| chrX | 157754834 | 157755334 |
| chrX | 159676288 | 159676788 |
| chrX | 160611271 | 160611771 |
| chrX | 162923562 | 162924062 |
| chrX | 166727871 | 166728371 |
| chrX | 167583004 | 167583504 |
| chrX | 168896638 | 168897138 |
| chrX | 169759712 | 169760212 |
| chrY | 1081618 | 1082118 |
| chrY | 1240276 | 1240776 |

## OCT4 peaks identified specifically in ESC and EpiLC (common)

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| chr1 | 4802450 | 4802950 |
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| chr1 | 4881790 | 4882290 |
| chr1 | 4934049 | 4934549 |
| chr1 | 5261214 | 5261714 |
| chr1 | 6117487 | 6117987 |
| chr1 | 6214251 | 6214751 |
| chr1 | 6282218 | 6282718 |
| chr1 | 6457904 | 6458404 |
| chr1 | 7020556 | 7021056 |
| chr1 | 7052241 | 7052741 |
| chr1 | 7088411 | 7089267 |
| chr1 | 7125003 | 7125503 |
| chr1 | 7125944 | 7126444 |
| chr1 | 7206162 | 7206662 |
| chr1 | 7207057 | 7207557 |
| chr1 | 7494035 | 7494535 |
| chr1 | 7671591 | 7672091 |
| chr1 | 7732635 | 7733135 |
| chr1 | 8496256 | 8496756 |
| chr1 | 8935954 | 8936454 |
| chr1 | 8940694 | 8941194 |
| chr1 | 9442903 | 9443403 |
| chr1 | 9545090 | 9545590 |
| chr1 | 9748225 | 9748725 |
| chr1 | 9954900 | 9955400 |
| chr1 | 10037763 | 10038263 |
| chr1 | 10650547 | 10651047 |
| chr1 | 11082094 | 11082594 |
| chr1 | 11147449 | 11147949 |
| chr1 | 11277021 | 11277521 |
| chr1 | 11277758 | 11278258 |
| chr1 | 11330123 | 11330623 |
| chr1 | 11395917 | 11396417 |
| chr1 | 11413944 | 11414444 |
| chr1 | 11501535 | 11502035 |
| chr1 | 12744420 | 12744920 |
| chr1 | 12807668 | 12808168 |
| chr1 | 12835974 | 12836474 |
| chr1 | 12886578 | 12887078 |
| chr1 | 12990950 | 12991450 |
| chr1 | 13051992 | 13052492 |
| chr1 | 13074359 | 13074859 |
| chr1 | 13308900 | 13309400 |
| chr1 | 13599762 | 13600262 |
| chr1 | 13938287 | 13938787 |
| chr1 | 14650311 | 14650811 |
| chr1 | 15791531 | 15792031 |
| chr1 | 16104562 | 16105062 |
| chr1 | 16129900 | 16130400 |
| chr1 | 16656869 | 16657369 |
| chr1 | 16823990 | 16825169 |
| chr1 | 17207376 | 17207876 |
| chr1 | 17531213 | 17531713 |
| chr1 | 17932113 | 17932613 |
| chr1 | 18639289 | 18639789 |
| chr1 | 20867308 | 20867808 |
| chr1 | 22377193 | 22377693 |
| chr1 | 23109088 | 23109588 |
| chr1 | 23922257 | 23922757 |
| chr1 | 24042930 | 24043430 |
| chr1 | 25012709 | 25013209 |
| chr1 | 25228494 | 25228994 |
| chr1 | 25242552 | 25243052 |
| chr1 | 26229669 | 26230169 |
| chr1 | 30414939 | 30415439 |
| chr1 | 33106264 | 33106764 |
| chr1 | 33494739 | 33495239 |
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| chr1 | 36890698 | 36891198 |
| chr1 | 36907153 | 36907653 |
| chr1 | 36984321 | 36984821 |
| chr1 | 36985824 | 36986324 |
| chr1 | 37049119 | 37049619 |
| chr1 | 37064534 | 37065034 |
| chr1 | 37890196 | 37890696 |
| chr1 | 38291478 | 38291978 |
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| chr1 | 39533884 | 39534384 |
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| chr1 | 40303086 | 40303586 |
| chr1 | 40680028 | 40680528 |
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| chr1 | 43098488 | 43098988 |
| chr1 | 43139507 | 43140007 |
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| chr1 | 43898891 | 43899801 |
| chr1 | 44102072 | 44102572 |
| chr1 | 44331687 | 44332187 |
| chr1 | 44701162 | 44701662 |
| chr1 | 44891565 | 44892065 |
| chr1 | 45795179 | 45795679 |
| chr1 | 45914245 | 45914745 |
| chr1 | 46853775 | 46854275 |
| chr1 | 48652521 | 48653021 |
| chr1 | 50637947 | 50638447 |
| chr1 | 50704613 | 50705113 |
| chr1 | 51478300 | 51478800 |
| chr1 | 52119183 | 52119683 |
| chr1 | 52431849 | 52432349 |
| chr1 | 52630656 | 52631156 |
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| chr1 | 53352377 | 53352877 |
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| chr1 | 53750794 | 53751294 |
| chr1 | 54250461 | 54250961 |
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# PUBLICATIONS

# ERF deletion rescues RAS deficiency in mouse embryonic stem cells

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**MEK inhibition in combination with a glycogen synthase kinase-3β (GSK3β) inhibitor, referred as the 2i condition, favors pluripotency in embryonic stem cells (ESCs). However, the mechanisms by which the 2i condition limits ESC differentiation and whether RAS proteins are involved in this phenomenon remain poorly understood. Here we show that RAS nullyzygosity reduces the growth of mouse ESCs (mESCs) and prohibits their differentiation. Upon RAS deficiency or MEK inhibition, ERF (E twenty-six 2 [Ets2]-repressive factor), a transcriptional repressor from the ETS domain family, translocates to the nucleus, where it binds to the enhancers of pluripotency factors and key RAS targets. Remarkably, deletion of *Erf* rescues the proliferative defects of RAS-devoid mESCs and restores their capacity to differentiate. Furthermore, we show that *Erf* loss enables the development of RAS nullyzygous teratomas. In summary, this work reveals an essential role for RAS proteins in pluripotency and identifies ERF as a key mediator of the response to RAS/MEK/ERK inhibition in mESCs.**

[*Keywords*: 2i; ERF; pluripotency; RAS; mESCs]

Supplemental material is available for this article.

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RAS proteins are small GTPases that are essential regulators of proliferation, differentiation, and survival in eukaryotic cells (Cox and Der 2010; Pylayeva-Gupta et al. 2011). These proteins oscillate between an active (GTP-bound) and inactive (GDP-bound) state that is in turn regulated by guanine exchange factors (GEFs; which promote the GDP/GTP exchange) and GTPase-activating proteins (GAPs; which accelerate GTP hydrolysis). RAS signaling initiates at the membrane, where it integrates cues coming from a wide range of mitogens such as epidermal growth factor (EGF) or fibroblast growth factors (FGF) through their cognate receptors. Upon activation, RAS proteins elicit their function by triggering several phosphorylation-based signaling pathways from which the RAF/MEK/ERK and PI3K/mTOR/AKT routes are the most studied. Ultimately, the RAS signal is executed by transcription factors, including FOS, JUN, MYC, and factors from the "E twenty-six" (ETS) domain family (Sizemore et al. 2017). While ETS domain factors are best known as activators of transcription, there are also examples of transcriptional repression. One such case is ERF (Ets2-repressive factor), which, in the presence of growth factors, is kept inactive in the cytoplasm by ERK-dependent phosphorylation and only translocates to the nucleus upon ERK inactivation to exert its function (Sgouras et al. 1995; Le Gallic et al. 1999).

Besides its well-established roles in regulating proliferation and survival in somatic cells, work with pluripotent cells has also revealed an important role of RAS signaling in promoting differentiation. Mouse embryonic stem cells (mESCs ) are characterized by their indefinite capacity to self-renew and differentiate into all cell types of the organism. In order to maintain their pluripotency, mESCs are cultured in the presence of leukemia inhibitory factor (LIF) and either bone morphogenetic protein 4 (BMP4) or fetal bovine serum (FBS) (Smith et al. 1988; Williams et al. 1988; Ying et al. 2003). Interestingly, ectopic expression of an activated H-RAS in mESCs leads to trophoectodermal differentiation, whereas interfering with FGF4-dependent MEK or ERK signaling impairs neuronal differentiation (Kunath et al. 2007; Lu et al. 2008). These experiments suggested that the RAS/MAPK pathway could be a primary trigger of cell commitment in ESCs. Accordingly, a combined inhibition of MEK and glycogen

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synthase kinase-3β (GSK3β), also known as the 2i condition, is sufficient to maintain pluripotency even in the absence of LIF and serum (Ying et al. 2008). However, regardless of the role of MEK, to what extent RAS proteins are involved in the exit from pluripotency has not been formally addressed. Our work presented here reveals an essential role of RAS proteins in the exit from pluripotency and identifies ERF as a key mediator of the response to RAS/MEK/ERK inhibition in mESCs.

## Results

### *The absence of RAS genes reduces the growth of mESCs*

To investigate the impact of RAS deficiency in pluripotent cells, we generated mESCs carrying constitutively null alleles for H-*Ras* and N-*Ras* and a conditional knockout K-*Ras* allele (H-*Ras*$^{-/-}$; N-*Ras*$^{-/-}$; K-*Ras*$^{lox/lox}$, referred to here as RAS$^{lox/lox}$) (Drosten et al. 2010). When combined with a Cre$^{ERT2}$ expressed from the locus of the large subunit of RNA polymerase II (Brocard et al. 1997), this system allows for the ablation of the remaining K-*Ras* allele upon addition of 4-hydroxytamoxifen (OHT) and thus the generation of mESCs devoid of all RAS proteins (RAS$^{less}$). The efficiency of the system was confirmed by Western blotting, which showed an efficient depletion of RAS after exposing RAS$^{lox/lox}$ mESCs to OHT, together with a severe reduction in the phosphorylation levels of MEK, ERK, and ribosomal S6 kinase (p90RSK), a well-established ERK target (Fig. 1A). In addition, gene set enrichment analysis (GSEA) from microarray data revealed an overall down-regulation of ERK/MAPK targets in OHT-treated RAS$^{lox/lox}$ mESCs (Fig. 1B; Supplemental Table 1). While MEK inhibition does not severely impair ESC growth (Li et al. 2007), the loss of all RAS proteins significantly reduced the size of mESC colonies (Fig. 1C), suggesting that *Ras* nullyzygosity could have a more profound impact on MEK/ERK signaling than chemical MEK inhibition. In support of this, the reduction in the phosphorylation levels of ERK and p90RSK was higher in RAS$^{less}$ cells than in mESCs treated with the MEK inhibitor PD0325901 (Supplemental Fig. S1A). Furthermore, while MEK inhibition

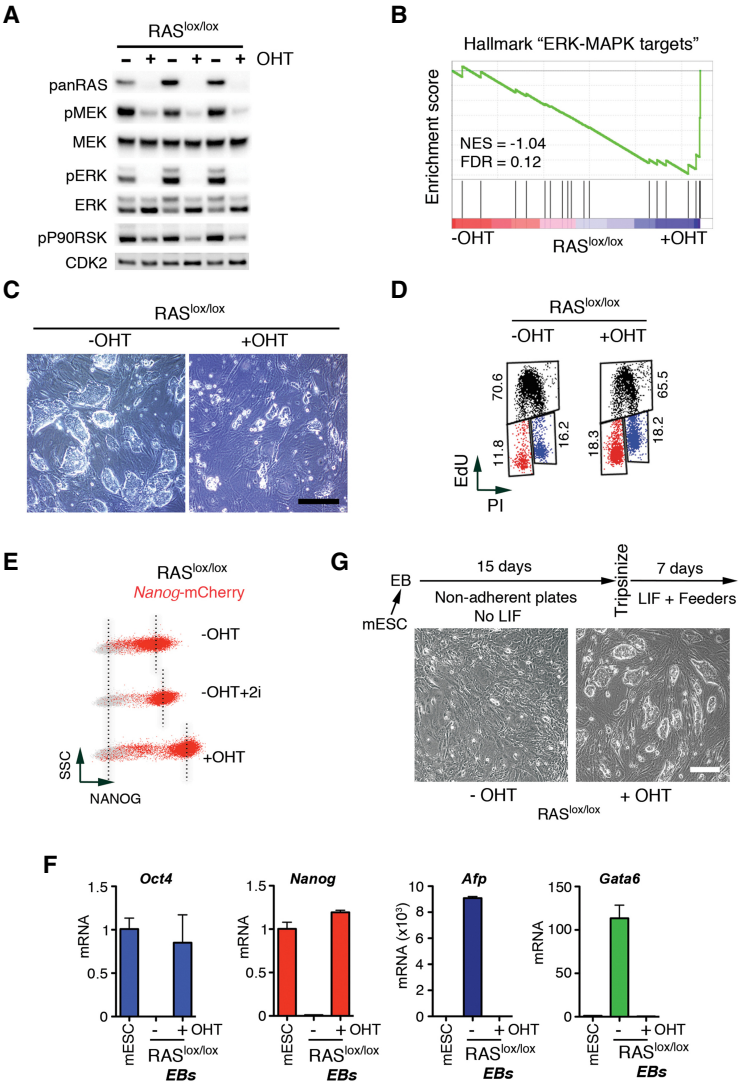


**Figure 1.** RAS deficiency impairs growth and differentiation in mESCs. (*A*) Western blot analysis illustrating the loss of the remaining K-RAS protein (with a panRAS antibody) and the decrease in the active phosphorylated forms of MEK, ERK, and P90RSK in OHT-treated (7 d) RAS$^{lox/lox}$ mESCs. Three independent RAS$^{lox/lox}$ mESC lines were used. CDK2 levels are shown as a loading control. (*B*) Preranked GSEA on the genes included in the hallmark "ERK–MAPK targets" revealed a down-regulation of the pathway in RAS-deficient mESCs. The heat map representation derives from two independent untreated or OHT-treated RAS$^{lox/lox}$ mESC lines 2 d after the addition of OHT. (*C*) Representative bright-field images corresponding to untreated or OHT-treated RAS$^{lox/lox}$ mESCs 7 d after the addition of OHT. Bar, 20 µm. (*D*) Flow cytometry analysis of the cell cycle distribution in untreated or OHT-treated RAS$^{lox/lox}$ mESCs 7 d after the addition of OHT. (*E*) Flow cytometry analysis of a knocked-in mCherry reporter at the *Nanog* locus in RAS$^{lox/lox}$ mESCs untreated, treated with OHT, and treated with 2i for 3 d. (*F*) mRNA levels of pluripotent (*Oct4* and *Nanog*) and differentiation (*Afp* and *Gata6*) markers in wild-type mESCs and in embryoid bodies (EBs) derived from untreated or OHT-treated RAS$^{lox/lox}$ mESCs as assessed by real-time PCR. *Gapdh* levels were used to normalize gene expression. Two independent experiments were performed, and data are shown as the averaged level of triplicates. Error bars indicate SD. (*G*) Representative bright-field images of the cultures initiated from EBs derived from untreated or OHT-treated RAS$^{lox/lox}$ mESCs that were maintained in suspension and in the absence of LIF for 15-d and subsequently trypsinized and plated on top of feeder mouse embryonic fibroblasts (MEFs) in mESC medium. Bar, 20 µm.

triggers a feedback loop that results in increased MEK phosphorylation (Caunt et al. 2015), the phosphorylation levels of MEK are sharply reduced in RAS$^{less}$ cells (Supplemental Fig. S1A).

To analyze the growth properties of RAS$^{less}$ mESCs, OHT-treated and untreated RAS$^{lox/lox}$ cells were infected with H2B-EGFP-expressing lentiviruses and video-monitored for 24 h at 10-min intervals. This analysis revealed that the reduced proliferation of RAS$^{less}$ cells was not due to an increase in cell death but rather the presence of cells that failed to progress into mitosis, consistent with the key role of MAPK signaling as a mitogenic pathway (Supplemental Fig. S1B). Flow cytometry analyses also did not show an increase of cell death in RAS$^{less}$ mESCs but revealed a slight arrest at the G1/S boundary (Fig. 1D). This phenotype is reminiscent of recent observations made in mESCs grown in 2i (Ter Huurne et al. 2017).

### *RAS deficiency prohibits mESC differentiation*

Next, we investigated the effects of RAS deficiency in pluripotency. Similar to the "ground state" achieved with the 2i condition (Ying et al. 2008), RAS$^{less}$ mESCs presented a more intense and homogeneous expression of NANOG and fewer differentiated colonies based on alkaline phosphatase activity (Supplemental Fig. S1C,D). Accordingly, flow cytometry analysis of a knocked-in mCherry reporter at the *Nanog* locus (Faddah et al. 2013) revealed that the loss of RAS genes in mESCs led to an increase in NANOG expression, which was actually higher than that achieved with the 2i condition (Fig. 1E). To evaluate the capacity of RAS-deficient mESCs to undergo differentiation, we first induced their differentiation toward intermediate mesoderm with a protocol based on retinoic acid and activin A (Oeda et al. 2013). This experiment revealed that RAS$^{less}$ mESCs induced to differentiate retained the expression of the pluripotency factors *Oct4* and *Nanog* and failed to express differentiation markers such as *Afp*, *Foxa2*, and *Msx1* (Supplemental Fig. S1E).

To further induce differentiation, we generated embryoid bodies (EBs) from OHT-treated or untreated RAS$^{lox/lox}$ mESCs and subsequently transferred them to gelatin-coated plates where they were left to differentiate for 10 additional days. Remarkably, even if RAS$^{less}$ mESCs were capable of generating EBs (see examples below), these EBs maintained the expression of *Oct4* and *Nanog* and failed to express differentiation markers such as *Gata4*, *Afp*, *Foxa2*, *Gata6*, and *Albumin* (Fig. 1F; data not shown). Finally, we tried to promote the differentiation of RAS$^{less}$ mESCs with the following experiment. EBs derived from untreated and OHT-treated RAS$^{lox/lox}$ mESCs were transferred to nonadherent plates in the absence of LIF and kept in suspension for 15 d, which is a highly stringent protocol, after which no pluripotent cells should remain. After this time, EBs were tripsinized and transferred to regular mESC culture plates containing feeders and LIF. As expected, no mESC colonies grew from trypsinized RAS-proficient EBs. In contrast, cultures initiated from RAS$^{less}$ EBs yielded abundant mESC colonies, confirming the incapacity of RAS-deficient mESCs to differentiate (Fig. 1G). Importantly, the lack of H-*Ras* and N-*Ras* present in RAS$^{lox/lox}$ cells does not significantly affect the self-renewal or differentiation capabilities of mESCs (Supplemental Fig. S2). Altogether, these experiments illustrate that the absence of RAS genes reduces the growth of mESCs and prevents their exit from pluripotency.

### *ERF deletion rescues growth and differentiation in RAS$^{less}$ mESCs*

In mammals, cumulative evidence supports an important role for ERF in counteracting the RAS signal (Sgouras et al. 1995; Le Gallic et al. 1999; Verykokakis et al. 2007). ERF is a transcriptional repressor from the ETS family that, in the presence of an active RAS/MEK/ERK pathway, is kept inactive in the cytoplasm through ERK-dependent phosphorylation and translocates to the nucleus upon ERK inhibition, leading to cell cycle arrest at G0/G1 (Le Gallic et al. 1999, 2004). Interestingly, ERF expression is particularly high in mESCs when compared with other cell types (Supplemental Fig. S3), suggesting a distinct function for this ETS domain factor in pluripotency. In support of this, exposure of mESCs to the 2i condition or the loss of *Ras* genes promoted the nuclear accumulation of ERF (Fig. 2A; Supplemental Fig. S4A,B). In addition, ERF phosphorylation levels were reduced in RAS$^{lox/lox}$ mESCs upon OHT treatment, further indicating its activation in RAS$^{less}$ cells (Fig. 2B). To evaluate whether ERF played a role in the reduced growth rates of RAS$^{less}$ cells, RAS$^{lox/lox}$ mESCs were infected with lentiviruses expressing Cas9 and two different single-guide RNAs (sgRNAs) targeting *Erf*. CRISPR-mediated depletion of ERF was efficient with both sgRNAs, as determined by Western blotting (Fig. 2B). ERF depletion fully rescued the growth of RAS$^{less}$ mESCs (Fig. 2C; Supplemental Fig. S4C). Video analysis of cell cycle progression confirmed the rescue of proliferation and mitotic entry rates that is achieved by *Erf* deletion in RAS-deficient mESCs (Supplemental Fig. S4D).

Next, we investigated whether ERF depletion could enable the differentiation of mESCs devoid of RAS genes by generating EBs. Consistent with the growth defects observed in RAS$^{less}$ cells, EBs generated from OHT-treated RAS$^{lox/lox}$ mESCs were smaller in size than RAS-proficient ones, an effect that was once again rescued by ERF depletion (Fig. 2D; Supplemental Fig. S4E). Subsequently, EBs were cultured on gelatin-coated plates, which leads to the growth of patches of differentiated cells that spread as a layer away from the EBs (Fig. 2E). In agreement with their incapacity to differentiate, RAS$^{less}$ EBs did not present such an outgrowth and stayed as compact EBs. In contrast, layers of emigrating cells were observed in the periphery of RAS$^{less}$ EBs that were also deficient in ERF (Fig. 2E), which expressed differentiation markers such as NESTIN (Supplemental Fig. S4F). ERF loss enabled a high degree of differentiation in RAS$^{less}$ cells, as exemplified by the observation of beating cardiomyocytes emerging from ERF-deficient RAS$^{less}$ EBs (Supplemental Movie 1).

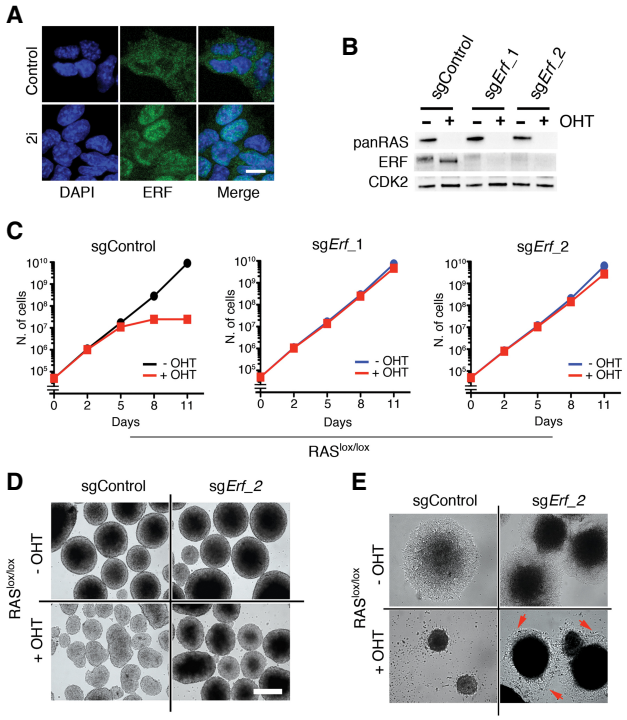


**Figure 2.** ERF loss rescues the effecs of RAS deficiency in mESCs. (*A*) Intracellular localization of ERF (green) in control or 2i-treated (2 h) wild-type mESCs. Bar, 5 µm. DAPI (blue) was used to stain DNA. (*B*) Western blot of ERF observed in untreated or OHT-treated (48 h) $RAS^{lox/lox}$ mESCs that had been infected with lentiviruses expressing Cas9 and sgRNAs against ERF (sg*Erf*_1 and *sgErf*_2) or a control sgRNA. The ERF band shift that occurs upon loss of all Ras proteins (detected with a panRAS antibody) is consistent with a loss of phosphorylation. CDK2 levels are shown as a loading control. (*C*) Cumulative growth curves from cultures of untreated or OHT-treated $RAS^{lox/lox}$ mESCs infected with lentiviruses expressing Cas9 and sgRNAs against ERF (sg*Erf*_1 and *sgErf*_2) or a control sgRNA. (*D*) Representative bright-field images from 4-d-old EBs maintained in suspension derived from untreated or OHT-treated $RAS^{lox/lox}$ mESCs infected with lentiviruses expressing Cas9 and sgRNAs against ERF (#2) or a control sgRNA. EB formation was initiated 5 d after the addition of OHT. Bar, 100 µm. (*E*) Representative bright-field images of 6-d-old EBs derived from untreated or OHT-treated $RAS^{lox/lox}$ mESCs infected with lentiviruses expressing Cas9 and sgRNAs against *Erf* (#2) or a control sgRNA that were subsequently plated onto gelatin to induce spontaneous differentiation. Bar, 100 µm.

### *ERF deletion enables the development of RAS nullyzygous teratomas*

Besides their role in pluripotency, *RAS* genes are best known as the most frequently mutated human oncogene (Pylayeva-Gupta et al. 2011). Given that RAS structural properties are unfavorable for the development of small molecule inhibitors (Cox et al. 2014), current therapies are oriented to target downstream effectors of RAS, such as RAF or MEK. However, resistance to these treatments invariably occurs due to the existence of numerous feedback loops (Samatar and Poulikakos 2014). In this context, even if potent and selective RAS inhibitors finally emerge, to what extent the anti-tumoral effects of these agents could also be bypassed by resistance mechanisms is not known. To evaluate the tumor formation potential of RAS-deficient mESCs, we generated teratomas. To this end, untreated and OHT-treated $RAS^{lox/lox}$ mESCs were injected subcutaneously into both flanks of nude mice. To discard variability between host mice, untreated mESCs were injected into one flank, and OHT-treated ones were injected into the other. Consistent with the major role of RAS in cancer, OHT-treated $RAS^{lox/lox}$ mESCs failed to form teratomas (Fig. 3A–C). In contrast, *Erf* deletion enabled the development of RAS-deficient teratomas (Fig. 3A–C). The size of ERF-deficient $RAS^{less}$ teratomas was similar to that of control tumors, further illustrating the extent of the synthetic viable effect that arises upon the concomitant loss of ERF and RAS (Fig. 3B; Supplemental Fig. S5A). Interestingly, one teratoma could be obtained from $RAS^{less}$ mESCs that were ERF wild type, which turned out to be a chimaera of RAS-proficient and RAS-deficient cells due to an incomplete OHT-induced deletion of the remaining K-*Ras* allele (Fig. 3D). Consistent with the incapacity of RAS-deficient mESCs to

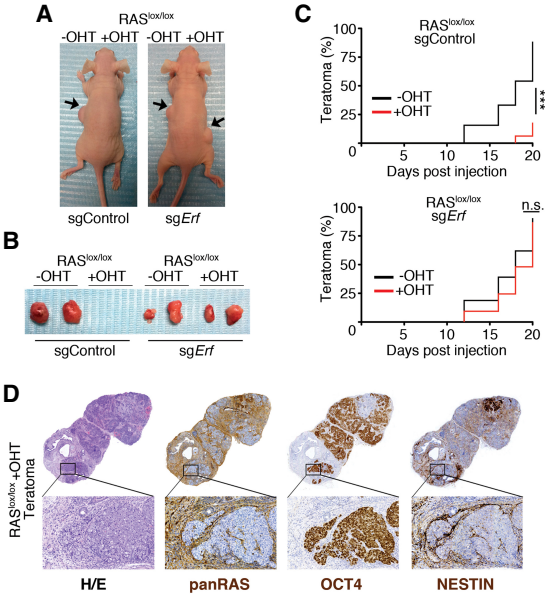


**Figure 3.** ERF deletion enables the development of RAS-devoid teratomas. (*A*) Representative images of mice bearing teratomas 20 d after the injection of untreated or OHT-treated $RAS^{lox/lox}$ mESCs infected with lentiviruses expressing Cas9 and sgRNAs against ERF or a control sgRNA. Eight mice were injected per condition. (*B*) Representative images of the teratomas obtained from the experiment defined in *A* at day 20. (*C*) Kaplan-Meier graphs illustrating the percentage of mice bearing teratomas after the injection of the indicated mESCs. (n.s.) Nonsignificant; (***) $P < 0.001$. (*D*) Immunohistochemistry of panRAS, OCT4, and NESTIN expression in the only teratoma obtained from OHT-treated $RAS^{lox/lox}$ mESCs that had been infected with a control sgRNA. Note that areas lacking panRAS staining retained OCT4 expression and failed to express NESTIN (zoomed-in square).

undergo differentiation, areas of this teratoma lacking RAS expression retained high levels of OCT4 and failed to express NESTIN, while differentiation could be readily observed in RAS-positive areas. Upon ERF loss, NESTIN-positive and OCT4-negative areas could be observed in RAS-deficient teratomas (Supplemental Fig. S5B). Moreover, ERF-deficient RAS nullyzygous teratomas presented areas of differentiation into all three embryonic layers (Supplemental Fig. S5C). In summary, these data demonstrate that *Erf* deletion enables the differentiation of mESCs devoid of all *Ras* genes in vitro and in vivo.

### *ERF is a regulator of transcriptional enhancers in mESCs*

To understand the mechanism by which ERF regulates growth and differentiation in mESCs, we mapped its genomic binding sites by chromatin immunoprecipitation (ChIP) followed by next-generation sequencing (ChIP-seq). To this end, we analyzed the chromatin association of ERF in $RAS^{lox/lox}$ mESCs that had been either treated or untreated with OHT for 7 d as well as in ERF-deficient mESCs as an antibody specificity control (Supplemental Fig. S6A). Consistent with the cytoplasmic localization of ERF in RAS-proficient cells, only one ERF peak could be detected in this condition (Supplemental Table 2). In contrast, 4297 potential ERF-binding sites were detected in OHT-treated $RAS^{lox/lox}$ mESCs (Supplemental Table 3). Interestingly, while ETS domain factors are most often associated with transcriptional control at promoter sites, a detailed analysis of ERF-bound sequences in $Ras^{less}$ mESCs showed that 45.5% of the peaks map to sequences 10–100 kb away from the transcription start site (TSS) (Fig. 4A). Moreover, the majority of ERF peaks is at either introns (36%) or intergenic sequences (45%) (Fig. 4B), similar to previous observations from an ERF ChIP-seq in growth-deprived mouse embryonic fibroblasts (MEFs) (Twigg et al. 2013).

The data above prompted us to explore whether ERF binding could preferentially occur at transcriptional enhancer sequences. To this end, we compared its distribution with a reference data set of 10,627 mESC enhancers (Hnisz et al. 2013), identifying ERF peaks in 1954 of these sites (Fig. 4C). Consistently, an independent statistical analysis identified that 49.1% all ERF peaks have a *P*-value of <0.05 for overlapping with mESC enhancer sequences (vs. randomly distributed) (see the Supplemental Material). Moreover, the distribution of ERF at these sites was similar to that of mESC enhancer-associated marks such as H3K4me1 and P300 (Fig. 4D,E; Heintzman et al. 2007). Interestingly and in addition to "negative regulation of MAPK cascade," gene ontology analyses identified "stem cell maintenance" and "blastocyst formation" among the most significantly enriched pathways harboring ERF-bound enhancers, highlighting a key role for ERF in the coordination of pluripotency (Supplemental Fig. S6B; Supplemental Table 4). In support of this, ERF bound to enhancer sequences present near the genes from core pluripotency factors such as OCT4 and KLF4 as well as from other factors with an important role in the maintenance of the ground state, such as ESSRB, NR5A2, PRDM14, TCFCP2L1, STAT3, and TCF3 (Fig. 4F; Hnisz et al. 2013; data not shown). Moreover, while motif analyses revealed ETS-binding sites as the most significantly enriched sequences at ERF peaks, this was followed in significance by the target sequences for OCT4, SOX2, and KLF4 (Supplemental Fig. S6C).

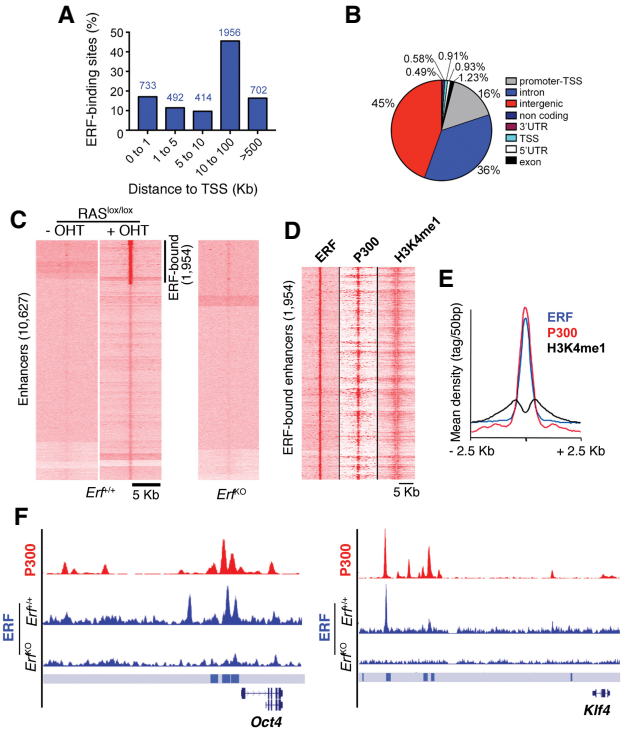


**Figure 4.** ERF binds to enhancers of RAS targets and pluripotency factors in mESCs. (*A*) Distribution of ERF-bound genomic regions in RAS-deficient mESCs related to the closest TSS. Numbers within the graph correspond to the number of ERF-bound genomic regions included in each category. (*B*) Distribution of the different genomic features overlapping with the 4297 ERF peaks identified in $RAS^{less}$ mESCs, identified with the HOMER bioinformatics package (see the Supplemental Material). (*C*) Heat map representations from untreated and OHT-treated $RAS^{lox/lox}$ mESCs of the normalized read density of the ERF ChIP-seq at 10,627 previously defined mESC enhancers (Hnisz et al. 2013). The heat map from the ERF ChIP-seq in $Erf^{KO}$ cells is provided as a control. (*D*) Heat map representation of the normalized read density of ERF ChIP-seq data around the 1954 enhancers bound by ERF in OHT-treated $RAS^{lox/lox}$ mESCs. The overlap with public ChIP-seq data sets of P300 (Gene Expression Omnibus [GEO] accession no. GSM918750) and H3K4me1 (GEO accession no. GSM1003750) distributions in mESCs is shown. (*E*) Average ERF, P300, and H3K4me1 ChIP-seq mean density distributions in mESCs as defined in *D*, centered around enhancers. (*F*) Representative ChIP-seq tracks of ERF at the *Oct4* (*left*) and *Klf4* (*right*) locus in $RAS^{less}$ mESCs. The ChIP-seq signal from ERF-deficient mESCs is also provided as a specificity control. The *X*-axis corresponds to the genomic location, and the *Y*-axis corresponds to normalized ChIP-seq signal density. The ChIP-seq track of P300 in mESCs (GEO accession no. GSM918750) is provided for comparison with a reference enhancer-associated mark. Known mESC enhancers are shown as blue boxes in the *bottom* track.

Regarding the impact of ERF binding in gene expression, bioinformatics analysis with the genomic enrichment of annotations tool (GREAT) (McLean et al. 2010) identified 5098 genes as associated with ERF peaks. When comparing this data set with microarray analyses of OHT-treated and untreated $RAS^{lox/lox}$ mESCs (Supplemental Table 1), 468 out of the 5098 genes (9.2%) that lay near ERF peaks were found to be down-regulated in RAS-deficient mESCs (Supplemental Table 5), consistent with the known role of ERF as a transcriptional repressor. Accordingly, ERF deletion increased the expression of the majority of genes that are down-regulated in $RAS^{less}$ mESCs and are in close proximity to ERF-bound enhancer regions (Supplemental Fig. S6D). This is exemplified by JARID2 or MYC, for instance, which present ERF peaks in the vicinity of their genes and are down-regulated in the absence of RAS in a manner that is alleviated by ERF deletion (Supplemental Fig. S6E–H). Besides *Myc*, the list of genes that present ERF peaks and are down-regulated in RAS-deficient mESCs includes key transducers of the RAS signal, such as *Pdk1*, the ETS domain factors *Etv1* and *Etv4*, and several negative regulators of growth factor signaling, including *Spred1*, *Dusp4*, *Dusp6*, *Spry2*, and *Spry4*. (Supplemental Table 5). Interestingly, 284 out of the 5098 genes (5.6%) associated with ERF peaks in $RAS^{less}$ mESCs presented increased expression in these cells, suggesting that ERF might also play an activating role at certain loci (Supplemental Table 6). In support of this, ERF deletion reduced the expression levels of many of the genes that are up-regulated in $RAS^{less}$ mESCs and are in close proximity to ERF-bound enhancers (Supplemental Fig. S6I). Thus, despite the well-established role of ERF as a transcriptional repressor (Sgouras et al. 1995; Le Gallic et al. 1999; Verykokakis et al. 2007), our current data indicate that the presence of ERF at mESC enhancers can either activate or repress transcription of the associated gene. Collectively, these data identify ERF as an enhancer-bound regulator of gene expression in pluripotent cells.

## Discussion

While RAS proteins are mostly known as oncogenic factors, the RAS/MEK/ERK axis also plays a key role in pluripotency. Accordingly, MEK inhibition or ERK1/2 deficiency limits the differentiation of mESCs (Ying et al. 2008; Chen et al. 2015). Our work further supports this concept, as mESCs devoid of RAS genes are completely incapable of abandoning pluripotency in vitro or in vivo. Still, how the inhibition of growth factor signaling favors pluripotency remains poorly understood. Here we identify ERF as member of the ETS family of transcription factors with a key role in this phenomenon. Upon loss of RAS proteins, ERF translocates to the nucleus, where it binds to a broad set of enhancers placed near key pluripotency and mitogenic factors. The localization of ERF at enhancers is consistent with recent ChIP-seq studies on ETS factors (Chen et al. 2013; Yang et al. 2015), which could indicate that this metazoan-specific family of transcriptional regulators might have evolved together with the emergence of enhancer sequences as modulators of their function. Given that ETS factors share a common binding sequence, it is possible that the presence of ERF upon inhibition of the RAS/MEK/ERK pathway impedes the recruitment of other ETS factors, thereby limiting their function.

The central role that ERF plays in restricting proliferation and differentiation in mESCs is unlikely to be determined by a single factor. Similar to what was reported for the 2i condition (Marks et al. 2012), reduced levels of MYC probably play an important role in the growth defects of $RAS^{less}$ mESCs. Accordingly, previous work identified MYC as a mediator of the growth-suppressing functions of ERF in MEFs (Verykokakis et al. 2007). Nevertheless, ERF binds to the enhancers of multiple members of the growth factor signaling pathway and ETS domain factors, some of which probably also contribute to the reduced growth rates of $RAS^{less}$ mESCs. As to how ERF restricts mESC differentiation, the polycomb repression complex 2 (PRC2) subunit JARID2 is an interesting candidate. Multilineage differentiation in mESCs depends on the transcriptional priming of developmental bivalent (H3K4me3/H3K27me3) genes by JARID2. Accordingly, JARID2 knockout mESCs have a severe compromised capacity to differentiate and are unable to intiate cell lineage commitment (Landeira et al. 2010). In this context, the finding that JARID2 levels are significantly down-regulated in RAS-deficient mESCs in an ERF-dependent manner provides an interesting mechanistic insight that could help in understanding how inhibition of the RAS/MEK/ERK pathway promotes a more ground state in mESCs. Besides the role of individual targets, ERF might also play a more general role in limiting mESC differentiation. Recent works have revealed that the transition from naïve to primed pluripotency involves a global reorganization of enhancer usage patterns for factors such as OCT4, which relocates from distal enhancers in naïve mESCs to more proximal enhancers in primed cells (Buecker et al. 2014; Factor et al. 2014). Likewise, OCT4, SOX2, and NANOG translocate to distal enhancers when mESCs are cultured under the 2i conditions (Galonska et al. 2015), suggesting that the "distal enhancer"-binding profile is a unique feature of ground-state mESCs. Given that ERF-bound enhancers are mostly distal, to what extent ERF binding mediates the global rewiring of enhancer usage associated with pluripotency emerges as an interesting possibility.

In regard to cancer, our work opens the unfortunate possibility that even if potent and selective RAS targeting drugs are finally developed, resistance mechanisms are likely to emerge. Supporting this concept, a recent study has shown that some pancreatic cancer lines can tolerate the absence of K-*RAS* (Muzumdar et al. 2017), although there could potentially be compensation from the rest of the members of the RAS family (Esteban et al. 2001; Potenza et al. 2005; Drosten et al. 2017). It is noteworthy that while H-*RAS*, N-*RAS*, and K-*RAS* are widely considered the main *RAS* genes in mammalian cells, mESCs express another variant, E-*Ras*, that could drive RAS signaling in pluripotent cells (Takahashi et al. 2003). However, the profound inhibition of MEK and ERK

phosphorylation in RAS$^{less}$ mESCs argues against E-*Ras* significantly contributing to RAS signaling in these cells (Fig. 1A; Supplemental Fig. S1A). In this context, while acknowledging that teratomas are a special tumor type, our data suggest that cancer cells might even be able to bypass RAS nullyzygosity through the inactivation of suppressors such as *ERF*. Interestingly, recurrent deletions and inactivating mutations of *ERF* have been found recently in prostate cancer (Bose et al. 2017; Dhingra et al. 2017; Huang et al. 2017). However, the impact of these mutations is still not fully characterized. Based on our work, it is tempting to speculate that loss of *ERF* function might increase the resistance to targeted therapies of the RAS/MEK/ERK pathway, including actual RAS inhibitors. Beyond the putative impact of ERF mutations in cancer, our work places ERF at the core of the response to RAS/MEK/ERK inhibition in pluripotent cells.

## Materials and methods

### *Mice*

Athymic nude Foxn1-null mice were obtained from Charles River. All mouse work was performed in the pathogen-free animal facility of the Spanish National Cancer Research Centre (CNIO) in accordance with the Guidelines for Humane Endpoints for Animals Used in Biomedical Research and under the supervision of the Ethics Committee for Animal Research of the "Instituto de Salud Carlos III."

### *Cell lines*

N-*Ras*$^{-/-}$; H-*Ras*$^{-/-}$; K-*Ras*$^{f/f}$; *Ubiq-Cre*$^{ERT2}$ (Drosten et al. 2010) and wild-type (R1 and G4) mESCs were grown on a feeder layer of growth-arrested MEFs or on gelatin at 37°C and 5% $CO_2$ in high-glucose DMEM (Invitrogen) supplemented with 15% FBS, 1000 U/mL LIF, 0.1 mM nonessential amino acids, 1% glutamax, 55 mM β-mercaptoethanol, and 1% penicillin/streptomycin unless otherwise indicated. MEFs were obtained from 13.5 embryos by standard methods. HEK293T (American Type Culture Collection) cells were grown in DMEM, 10% FBS, and 1% penicillin/streptomycin.

### *mESC differentiation*

For differentiation toward intermediate mesoderm, dissociated RAS$^{lox/lox}$ mESCs (untreated or OHT-treated previously for at least 5 d) were seeded without feeders on gelatin-coated plates and cultured in DMEM supplemented with 10% FBS, 0.1 mM nonessential amino acids, 55 mM β-mercaptoethanol, 1% penicillin/streptomycin, and 10 ng/mL activin A for 4 d as described previously (Oeda et al. 2013). In the last 2 d, 50 nM retinoic acid was also added to the culture medium.

### *EBs*

To generate EBs, trypsinized ERF-proficient and ERF-deficient RAS$^{lox/lox}$ mESCs (untreated or OHT-treated previously for at least 5 d) were hanging drop-cultured at a density of 60,000 cells per milliliter for 2 d. After this time, cells were collected and cultured in suspension in low-attachment plates in DMEM without LIF supplemented with 10% FBS, 0.1 mM nonessential amino acids, 55 mM β-mercaptoethanol, and 1% penicillin/streptomycin. To further induce differentiation, EBs were transferred to gelatin-coated plates and left to differentiate for 10 additional days in the same medium condition.

### *Teratoma formation*

mESCs ($1 \times 10^6$) were subcutaneously injected into the flanks of nude Foxn1-null mice and inspected daily for a period of several weeks to assess teratoma growth and size (measures were calculated according to the formula length × width$^2$ × 0.5). Eight independent injections per group were performed.

### *Plasmids*

The lentiviral plasmid pLentiCRISPRv2 (Addgene, 52961) was used to express sgRNAs. The sequences of the sgRNAs used were designed with the Massachusetts Institute of Technology CRISPR design tool (http://www.genome-engineering.org/crispr). pLenti-H2B-EGFP was a kind gift from Dr. Marcos Malumbres (CNIO). The plasmid Nanog-2A-mCherry (Addgene, 59995) was used to knock in a mCherry cDNA at the *Nanog* locus.

### *High-throughput microscopy*

High-throughput microscopy for the analysis of ERF nuclear translocation was performed as described previously with antibodies against endogenous ERF (see Supplemental Table 7 for a list of antibodies used in this study; Lopez-Contreras et al. 2012). Briefly, images from each well were automatically acquired by an Opera high-content screening system (Perkin Elmer) at nonsaturating settings and segmented using DAPI staining to generate masks matching cell nuclei. Upon quantification of ERF signals, a nuclear/cytoplasmic ratio was established for each cell. Where the observed ratio was above the values found in 95% of untreated mESCs, the cells were considered to have a "nuclear" localization of ERF. Data were represented with Prism (GraphPad Software).

### *ChIP-seq and microarray data*

Microarray and ChIP-seq data are available at the NCBI Gene Expression Omnibus under accession number GSE99477. Bioinformatics analyses and experimental methods for ChIP-seq and microarray experiments are detailed in the Supplemental Material.

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# ERF deletion rescues RAS deficiency in mouse embryonic stem cells

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# The ETS Transcription Factor ERF controls the exit from the naïve pluripotent state in a MAPK-dependent manner

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**ABSTRACT**

The naïve epiblast transitions to a pluripotent primed state during embryo implantation. Despite the relevance of the FGF pathway during this period, little is known about the downstream effectors regulating this signaling. Here, we examined the molecular mechanisms coordinating the naïve to primed transition by using inducible ESC to genetically eliminate all RAS proteins. We show that differentiated $RAS^{KO}$ ESC remain trapped in an intermediate state of pluripotency with naïve-associated features. Elimination of the transcription factor ERF overcomes the developmental blockage of RAS-deficient cells by naïve enhancer decommissioning. Mechanistically, ERF regulates NANOG expression and ensures naïve pluripotency by strengthening naïve transcription factor binding at ESC enhancers. Moreover, ERF negatively regulates the expression of the methyltransferase DNMT3B, which participates in the extinction of the naïve transcriptional program. Collectively, we demonstrated an essential role for ERF controlling the exit from naïve pluripotency in a MAPK-dependent manner during the progression to primed pluripotency.

**Teaser**: ERF is the MAPK-dependent switch controlling the transition between naïve and primed pluripotency.

## INTRODUCTION

Embryonic cells residing within the inner cell mass (ICM) are pluripotent as they have the potential to generate all cell lineages of the organism. The state of pluripotency found in the pre-implantation epiblast, prior to any lineage specification, is usually defined as naïve (*1*). However, as the embryo expands and develops after implantation, epiblast cells become individually fated, although still retain pluripotent features. This state of pluripotency associated with the post-implantation epiblast is defined as primed (*2, 3*). More than distinct pluripotent states, naïve and primed can be viewed as different phases of a coordinated developmental progression where naïve unbiased cells differentiate responding to inductive cues to initiate a multi-lineage decision commitment at gastrulation (*2, 3*).

Naïve and primed pluripotent states can be captured *in vitro* by defined culture conditions. Mouse embryonic stem cells (ESC) can be propagated in naïve conditions by using a combination of a MEK inhibitor (PD0325091) plus a glycogen synthase kinase-3 inhibitor (CHIR99021; hereafter referred as the 2i condition) (*4*). ESC grown under these conditions resemble embryonic cells residing in the pre-implantation embryonic (E) post-fertilization day E3.5-E4.25 embryo and have been extensively used to study the ground state of pluripotency. In addition, cultures of embryonic cells that retain primed pluripotency can also be established from post-implantation embryos (*5*). These epiblast stem cells (EpiSC) are developmentally similar to the ectoderm of late-gastrula embryo and display anterior primitive streak properties (*6*). Both types of cells, naïve and primed, share the expression of core pluripotent transcription factors (TF), such as OCT4 and SOX2. However, 2i-ESC express specific naïve TF (REX1, NANOG or KLF4), which are absent in EpiSC, whereas EpiSC express epiblast specific genes (OCT6 or OTX2), absent in ESC. Importantly, these pluripotent cell types are interconvertible by modifying the culture conditions or expressing specific TF (*3*). Recently, a distinct intermediate state of pluripotency has been identified, the rosette pluripotent state (*7*). Rosette embryonic stem cells (RSC) co-express naïve TF and the primed marker OTX2. Inhibition of WNT signaling drives the pluripotent transition from naïve to the rosette state while further activation of the RAS/MAPK signaling promotes the progression to primed pluripotency (*7*). Furthermore, additional states of intermediate pluripotency characterized by germ cell specification capacity have also been described:

formative stem cells (FSC), formative pluripotent stem cells (fPSC) and chimera pluripotent stem cells (XPSC) (*8-10*). These intermediates rely on exogenous (XPSC, fPSC) or autocrine (FSC) FGF signaling for their self-renewal in contrast to the requirements for RSC. In summary, pluripotency can be considered as a dynamic property associated with different stem cell states supported by defined pluripotent transcriptional networks.

Exit from naïve pluripotency during implantation is essential to fate epiblast cells residing in the ICM with inductive signals prior to gastrulation. However, the molecular mechanisms coordinating the naïve to primed transition are not fully understood. Moreover, despite the relevance of the RAS pathway during this critical period, little is known about the downstream effectors regulating the MAPK transcriptional program. We recently identified the transcriptional repressor ERF, a member of the E26 transformation specific (ETS) family, as an important regulator downstream of the RAS pathway in ESC (*11*). ERF is a TF that shuffles between the nucleus and cytoplasm in ESC in a phosphorylation-dependent manner (*12*). In the absence of RAS/MAPK signaling, ERF remains unphosphorylated and chromatin-bound in the nucleus while growth factor stimulation keeps ERF inactive in the cytoplasm by ERK-dependent phosphorylation (*12-14*). Importantly, the precise role of ERF during early embryonic development and pluripotent transitions is unclear. Here, we show that ERF plays a dual role in the transition from naïve to primed pluripotency. First, ERF binds to ESC super-enhancers to ensure optimal expression of naïve TF in the absence of FGF signaling. Second, activation of MAPK signals induces the release of chromatin-bound ERF, an event that is necessary and sufficient to trigger full commitment to primed pluripotency. In addition, we also show that ERF controls the expression of the *de novo* methyltransferase DNMT3B through LIN28 regulation, leading to the inactivation of the naïve transcriptional program. Our data demonstrate that ERF is the MAPK-dependent switch that controls the progression to primed pluripotency.

## RESULTS

### ERF is expressed in the naïve pluripotent epiblast

We first sought to determine the precise expression timing for ERF during embryonic development. For this, we collected mouse embryos at different developmental stages and performed immunofluorescence analyses. We determined that ERF expression peaks around E3.5-E4.0 and is coincidental with the naïve pluripotent epiblast (Fig. 1, A to C, and fig. S1A). ERF is expressed in the naïve inner cell mass (ICM) and co-expressed with the naïve pluripotent markers NANOG and KLF4 (Fig. 1, B and C, fig. S1A). In addition, we also detected ERF in the trophectoderm (TE), consistent with its reported requirement for chorionic trophoblast differentiation, but with negligible expression in the primitive endoderm (Fig. 1, B and C, and fig. S1B) (*15*). Exit from naïve pluripotency *in vivo* and downregulation of naïve associated markers strongly correlated with decreased expression of ERF (Fig. 1, B and C, fig. S1A). We confirmed this expression pattern by analyzing single-cell RNAseq datasets from embryos at different stages (fig. S2, A and B) (*16*). These results showed that ERF is upregulated during ICM formation and it is quickly downregulated before implantation, suggesting a role for ERF in the naïve epiblast.

To validate our observations and assess the role of the MAPK pathway in ERF levels, we used an ESC model deficient in H-RAS and N-RAS with a conditional knockout K-RAS triggered by the addition of 4-hydroxytamoxifen (OHT) ($RAS^{lox/lox}$ hereafter) (*11, 17*). These ESC allowed us to generate cells devoid of all RAS proteins. We next applied a well-established *in vitro* protocol using FGF2 and Activin-A (FA, hereafter) to differentiate naïve ESC, growing in 2i+LIF (2iL) conditions, to post-implantation epiblast like cells (EpiLC) and examined ERF levels (*18, 19*). While $RAS^{lox/lox}$ 2iL-ESC showed high levels of ERF, these cells exhibited negligible levels when differentiated into EpiLC (Fig. 1D). ERF is quickly phosphorylated upon differentiation and the decrease in protein levels is due to transcriptional repression (fig. S2C) (*20*). We next examined whether this downregulation depended on FGF/MAPK activation. Indeed, RAS-deficient cells ($RAS^{KO}$) retained elevated levels of ERF after differentiation (Fig. 1D). Together, these results pointed to a role for ERF in the exit from naïve pluripotency in a MAPK-dependent manner.

**Downregulation of ERF is necessary for the successful exit from naïve pluripotency**

To evaluate the implication of ERF in the exit from naïve pluripotency, we examined its expression along with markers of naïve pluripotency during the formation of embryonic rosettes. In this assay, single cell suspensions of ESC embedded in Matrigel exit from naïve pluripotency and develop into polarized rosettes that undergo lumenogenesis, mimicking the morphogenic events of the epiblast (*21*). This *in vitro* system recapitulates the development of the ICM during peri-implantation. Importantly, ESC rosettes generated under 2iL conditions lack lumen, continue to express naïve markers, and eventually become disorganized over time (*22*). This showed that exit from naïve pluripotency is necessary for successful polarization and lumenogenesis. Upon 2iL removal and resuspension in Matrigel, $RAS^{lox/lox}$ rosettes showed polarization and lumen, expression of the sialomucin protein podocalyxin (PDX) and downregulation of the naïve marker NANOG (Fig. 2, A to C, and fig. S3, A and B). However, $RAS^{KO}$ rosettes developed into a disorganized group of cells, which lacked expression of PDX and retained naïve pluripotency markers (Fig. 2, A to C, and fig. S3, A and B). It has been shown that WNT inhibition promoted rosette formation while further MEK inhibition promoted lumen formation (*7*). Thus, it is possible that $RAS^{KO}$ ESC still retain elevated levels of WNT signaling when placed in Matrigel, which will impair rosette formation. To examine whether $RAS^{KO}$ ESC have the ability to form rosettes, we cultured $RAS^{lox/lox}$ and $RAS^{KO}$ ESC with or without the WNT inhibitor IWR-1. While $RAS^{lox/lox}$ ESC still developed embryonic rosettes, $RAS^{KO}$ ESC are unable to organize a rosette even in the absence of WNT signaling suggesting that RAS signaling is necessary for both, rosette and lumen formation (fig. S3, C and D). To test whether ERF regulates the exit from naïve pluripotency, we generated ERF-knockouts ($ERF^{KO}$) and evaluated rosette formation in all different genotypes ($RAS^{lox/lox}$, $ERF^{KO}$, $RAS^{KO}$, and $RAS^{KO}$; $ERF^{KO}$). Elimination of ERF is sufficient to induce exit from naïve pluripotency and to rescue, in most of the embryonic rosettes, the failed morphogenic events (polarization and lumenogenesis) observed in $RAS^{KO}$ rosettes (Fig. 2, A to C, and fig. S3A and B). To further support these observations, we generated reporter cell lines in our ESC by replacing the endogenous coding sequence of the gene REX1 (also known as ZFP42) with a short half-life form of eGFP (REX1-deGFP). Similar REX1-deGFP reporter ESC have been widely used as

a faithful system to monitor exit from naïve pluripotency (*23*). Induction of EpiLC by FA in $RAS^{lox/lox}$ and $ERF^{KO}$ ESC demonstrated efficient downregulation of the reporter while $RAS^{KO}$ ESC showed no signs of downregulation (Fig. 2D). However, exit from naïve pluripotency was efficiently achieved in $RAS^{KO}$; $ERF^{KO}$ ESC (Fig. 2D). Finally, we also examined the clonogenicity potential of $RAS^{KO}$; $ERF^{KO}$ ESC primed to exit naïve pluripotency. For this, cultures of ESC ($RAS^{lox/lox}$, $ERF^{KO}$, $RAS^{KO}$, and $RAS^{KO}$; $ERF^{KO}$) were withdrawn from 2iL for 2 days and plated back in 2iL conditions for a colony forming assay. Cells that exit naïve pluripotency are irreversibly committed and have lost the ability to generate colonies in 2iL conditions. Indeed, while $RAS^{KO}$ ESC were able to generate alkaline phosphatase positive colonies and remained trapped in a naïve pluripotent state, $RAS^{KO}$; $ERF^{KO}$ ESCs lost this ability (Fig. 2E). Our results demonstrate a predominant role for ERF controlling the exit from naïve pluripotency in a MAPK-dependent manner.

**ERF controls the progression to primed pluripotency in a MAPK-dependent manner**

To obtain mechanistic insights into the rescue mediated by the loss of ERF during the exit from naïve pluripotency, we performed RNA sequencing (RNAseq) analysis of ESC cultured under naïve conditions (2iL) or differentiated into EpiLC in FA. Principal component plot (PCA) analysis segregated the samples based on their differentiation status alongside PC1, and MAPK activity alongside PC2 (Fig. 3A, and fig S4, and Supplementary Data S1). Interestingly, FA-$RAS^{KO}$ ESC are localized at an intermediate state between naïve and primed pluripotency (Fig. 3A, and fig S4). FA-$RAS^{KO}$ ESC are characterized by the intermediate to high expression of naïve pluripotent markers as well as of primed associated genes including OTX2 (Fig. 3, B and C, and fig S4). Indeed, while naïve pluripotent ESC are characterized by a $NANOG^{+}/OTX2^{-}/OCT6^{-}$ state, FA-$RAS^{KO}$ ESC showed a $NANOG^{+}/OTX2^{+}/OCT6^{-}$ state (Fig. 3, B and C). Furthermore, although FA-$RAS^{lox/lox}$ ESC have undetectable levels of ERF upon differentiation, FA-$RAS^{KO}$ ESC retain high ERF expression (Fig. 3C). Interestingly, FA-$RAS^{KO}$ ESC co-express OTX2, ERF and NANOG showing heterogenous levels between individual cells (fig. S5, A and B). Using available datasets that evaluate temporal transcriptional dynamics during the transition from naïve to primed pluripotency, we determined that FA-$RAS^{KO}$ ESC transcriptionally resembled that of ESC primed for 12-24 hours (Fig. 3D and fig. S5C) (*20*). Interestingly, FA-$RAS^{KO}$ ESC are reminiscent of the recently described intermediate

pluripotent states, rosette and formative pluripotent states (fPSC, RSC, FSC and XPSC) (*7-10*). PCA analyses showed that PC1 (differentiation status) placed all intermediate pluripotent states in a similar transcriptional space but PC2 segregated FA-RAS$^{KO}$ ESC from rosette or formative pluripotent states (Fig. 3E). Hierarchical clustering analysis based on the expression of naïve and primed markers revealed that RSC and FA-RAS$^{KO}$ ESC are transcriptionally more comparable, likely to the defective MAPK signaling in both intermediate states (Fig. 3F). Finally, we observed that FA-RAS$^{KO}$ ESC in FGF2/Activin-A/XAV939 (FAX) conditions were stably propagated for more than 15 passages demonstrating their trapping in this intermediate state of pluripotency (fig. S5D). Cultured FAX-RAS$^{KO}$ ESC also showed heterogenous levels of OTX2, ERF and NANOG between individual cells suggesting that these cells might fluctuate between different transcriptional states (fig. S5D). Importantly, FAX-RAS$^{KO}$ ESC can revert back to a naïve pluripotent state when transferred to 2iL conditions demonstrating that this intermediate state is reversible (fig. S6). Our results showed that loss of ERF is necessary and sufficient to overcome the developmental blockage of FA-RAS$^{KO}$ ESC in its intermediate pluripotent state. Indeed, RNAseq data revealed that loss of ERF in RAS$^{KO}$; ERF$^{KO}$ ESC restored the overall gene expression profile to be indistinguishable from FA-RAS$^{lox/lox}$ (Fig. 3, A and B, and fig. S4). Collectively, our data point to ERF as the MAPK-dependent switch that triggers full commitment to primed pluripotency.

**Chromatin-bound ERF ensures an optimal naïve pluripotency state**

The expression of ERF correlates with high expression levels of naïve markers *in vivo* and *in vitro* and is quickly downregulated upon induction to primed pluripotency (Fig. 1). Moreover, ERF is enriched in a total of 2074 bona-fide ESC enhancers identified in RAS$^{KO}$ ESC (2074/5529 total ERF peaks, fig. S7A and Supplementary Data S2 and S3) (*11*). Among these, ERF binds to most of the super-enhancers identified in ESC (198/231) (Supplementary Data S4) (*11*, *24, 25*). ERF-bound super-enhancers are associated to highly transcribed naïve genes (KLF4, ESRRB, PRDM14, NANOG, TBX3 or ZFP42) (some examples in fig. S7B) as well as to general pluripotent genes (OCT4 or SOX2). Although ERF is considered to be a transcriptional repressor, we hypothesized that ERF might play a different role at ESC enhancers. To explore the relevance of ERF at these enhancers,

we first examined the level of occupancy of the pluripotent transcription factors OCT4, SOX2 and NANOG (O, S and N, respectively) in the subset of ERF-bound 2074 ESC enhancers. We observed increased occupancy of bound OSN at these compared to a non-ERF bound randomized set of different 2074 enhancers (Fig. 4A). In addition, ERF-bound ESC enhancers are also characterized by higher H3K27Ac levels, increased p300 binding and chromatin accessibility detected by ATACseq (fig. S7C). These results suggested that ERF could be regulating the activity of these enhancers, and thus, the expression of their associated genes. Therefore, we examined the expression levels of essential naïve pluripotent genes associated to ERF-bound super-enhancers in $RAS^{lox/lox}$ and $ERF^{KO}$ ESC grown in 2iL conditions. Interestingly, NANOG, PRDM14 and ZFP42 showed decreased expression in 2iL-$ERF^{KO}$ ESC, while TBX3, KLF4 and ESRRB do not (Fig. 4B). It has been shown that NANOG promotes chromatin accessibility and binding of pluripotent factors to enhancers (*26*). Thus, we hypothesized that reduced levels of NANOG could affect the expression of additional naïve-associated genes. Indeed, $ERF^{KO}$ cells showed an overall decreased expression of the naïve pluripotent transcriptional network (Fig. 4C). Consistent with these results, unidimensional PCA analysis (PC1) segregating samples based on their differentiation status showed that 2iL-$ERF^{KO}$ ESC are biased toward differentiation (Fig. 4D). These combined results revealed that ESC growing under naïve conditions required ERF binding at enhancers to maintain an optimal naïve pluripotent state. To confirm this observation, we employed native Cut&Run sequencing to examine SOX2 and NANOG occupancy in $RAS^{lox/lox}$ and $ERF^{KO}$ ESC grown in 2iL conditions. As predicted, both pluripotent transcription factors showed an overall decreased enrichment in ESC enhancers in naïve $ERF^{KO}$ ESC (Fig. 4, E and F, and fig. S7D). These data support our findings and revealed an unexpected unique role for ERF in promoting naïve pluripotency.

**The naïve enhancer landscape is active in FA-$RAS^{KO}$ ESC**

Inactivation of the naïve transcriptional network is necessary for the successful progression to primed pluripotency. This is associated with decommission of naïve enhancers by downregulation of naïve transcription factors including ESRRB, KLF4 or NANOG and a widespread OCT4 genomic relocation (*27*). Indeed, OCT4 shifts from enhancers associated with key players

in naïve pluripotency and engages in new enhancer elements at genes implicated in post-implantation development. Using datasets for OCT4 occupancy in ESC and EpiLC and based on the relative occupancy between both cellular states, we defined top OCT4 sites preferentially enriched in ESC (4759 sites, $OCT4^{ESC}$), EpiLC (2921 sites, $OCT4^{EpiLC}$) and commonly shared between the two (9144 sites, $OCT4^{Common}$) (fig. S8A, and Supplementary Data S5-7). Genes associated with $OCT4^{ESC}$ sites are mostly downregulated during the transition to primed pluripotency whereas genes associated to $OCT4^{EpiLC}$ sites are upregulated (*27*). Out of all OCT4 bound sites, a total of 12.52% (596/4759 ERF/$OCT4^{ESC}$ sites), 13.62% (1246/9144 ERF/$OCT4^{Common}$ sites) and 0.15% (44/2921 ERF/$OCT4^{EpiLC}$ sites) were co-occupied by ERF in naïve ESC (Fig. 5A). This suggested that ERF does not play a specific role in genes associated with EpiLC-specific sequences but instead in regulating $OCT4^{ESC}$ and $OCT4^{Common}$ sites. We first focused on $OCT4^{ESC}$ sites as we observed that FA-$RAS^{KO}$ ESC remain trapped in an intermediate state between naïve and primed pluripotency and showed expression of naïve pluripotent markers (Fig. 3, A to C). Differentially expressed genes associated with ERF/$OCT4^{ESC}$ sites were mostly downregulated during FA differentiation in $RAS^{lox/lox}$ ESC (Fig. 5B). While many of these genes did not change their expression level in FA-$RAS^{KO}$ ESC, those that changed showed a lower extent of differential expression (Fig. 5B). Enhancer decommission of naïve enhancers by OCT4 relocation is followed by changes in enhancer chromatin patterns including decreased levels of H3K27ac (*27*). Thus, we examined whether the naïve enhancer landscape is still fully active in FA-$RAS^{KO}$ ESC by performing native Cut&Run sequencing to evaluate the levels of H3K27ac as a marker for active enhancers and NANOG occupancy in ESC and EpiLC from all genotypes. Interestingly, 2iL-$RAS^{KO}$ ESC showed increased acetylation and NANOG occupancy at ERF/$OCT4^{ESC}$ sites (Fig. 5, C and D), a phenotype that is also observed in all $OCT4^{ESC}$ sites (fig. S8B). This increase in H3K27ac levels does not result in major overall transcriptional changes and the expression level of naïve associated genes is similar between $RAS^{lox/lox}$ and $RAS^{KO}$ ESC (Fig. 4C). This observation supports the idea that levels of H3K27ac does not necessarily determine enhancer activity but rather discriminates between active or poised enhancers (*28*). Exit from naïve pluripotency correlated with an overall decrease in H3K27ac levels, negligible chromatin-bound NANOG and reduced expression of naïve-associated genes in $RAS^{lox/lox}$ ESC (Fig. 5, C and D, and fig. S8B). However, FA-$RAS^{KO}$ ESC showed

elevated gene expression, NANOG occupancy and H3K27ac levels at ERF/OCT4$^{ESC}$ sites to, in some cases, a comparable level as detected in naïve RAS$^{lox/lox}$ ESC (Fig. 5, C and D). Together, these data showed that naïve-specific associated OCT4 binding sites remain fully active in the FA-RAS$^{KO}$ ESC intermediate state.

We next focused specifically on the regulatory sequences and expression level of naïve transcription factors associated with ERF-bound super-enhancers. Among these, the expression level of ERF-dependent genes (NANOG, PRDM14 and ZFP42) is unaffected in FA-RAS$^{KO}$ ESC and is comparable to that of RAS$^{lox/lox}$ ESCs as ERF is still expressed (Fig. 5E). However, ERF-independent genes (ESRRB, TBX3 and KLF4) showed a significant decrease in expression, suggesting that additional mechanisms ensure optimal expression of these genes in 2iL-ESC (Fig. 5E). Collectively, these results demonstrated that FA-RAS$^{KO}$ ESC retain an active naïve transcriptional network. Although some naïve markers showed a marked decreased expression at this stage, elevated levels of NANOG, PRDM14 or ZFP42 likely sustain the naïve like-state in FA-RAS$^{KO}$ ESC mediated by ERF-dependent mechanisms.

**OTX2 co-occupies binding sites with NANOG in FA-RAS$^{KO}$ ESC**

Global reorganization of OCT4 genomic binding is driven by increased expression of OTX2 during naïve to primed transition (*27*). In fact, ectopic OTX2 expression in 2iL-ESC shows that it behaves as a pioneering factor engaging in previously inaccessible enhancer sites, relocates OCT4 to these sites, and induces the expression of primed-associated genes (*27*). OTX2 expression is independent of MEK signals but is efficiently repressed by the WNT pathway, thus explaining the elevated levels of OTX2 in rosette-like ESC (*7*). High levels of OTX2 have also been found to be associated with formative pluripotency (*7-10*). In addition, we also detected similar high OTX2 levels in FA-RAS$^{KO}$ ESC compared to FA-RAS$^{lox/lox}$ (Fig. 6A). We have shown that ERF binding sustains optimal naïve transcription factor expression (Fig. 4) and thus, we asked whether ERF is involved in OTX2 regulation. Indeed, ERF binds to the super-enhancer region associated with OTX2 in RAS$^{KO}$ ESC. Furthermore, the low levels of OTX2 expression observed in 2iL-RAS$^{lox/lox}$ ESC are further decreased in 2iL-ERF$^{KO}$ ESC (Fig. 6, A and B). This decrease correlates with lower NANOG and SOX2 binding and suggests that ERF binding might prevent further OTX2 repression

in the absence of FGF signaling (Fig. 6B). In agreement, FA-RAS$^{KO}$ ESC showed strong NANOG enrichment as well as OTX2 itself, which could potentially sustain its own expression after NANOG downregulation (fig. S9A). We next focused on the ERF/OCT4$^{Common}$ sites as they gained OTX2 and H3K27ac enrichment in EpiLC compared to ESC (*27*). Differentially expressed genes associated with ERF/OCT4$^{Common}$ sites were mostly upregulated in FA-RAS$^{lox/lox}$ (Fig. 6C). Similar to what we observed with genes associated with ERF/OCT4$^{ESC}$ sites, many of these genes did not change their expression levels in FA-RAS$^{KO}$ ESC and those that changed showed a lower differential expression extent (Fig. 6C). Based on the elevated levels of NANOG expression in FA-RAS$^{KO}$ ESC, we hypothesized that ERF/OCT4$^{Common}$ sites also retained chromatin bound NANOG. While FA-RAS$^{lox/lox}$ showed negligible enrichment of NANOG at these sites, FA-RAS$^{KO}$ ESC retained NANOG bound (Fig. 6D). In addition, we also observed stronger OTX2 enrichment at these sites in FA-RAS$^{KO}$ ESC compared to FA-RAS$^{lox/lox}$ (Fig. 6D). Interestingly, we also detected OTX2 binding in FA-RAS$^{KO}$ ESC at the ERF/OCT4$^{ESC}$ sites, naïve associated sequences that are decommissioned during the transition to EpiLC (Fig. 6D). These observations were also confirmed globally in all OCT4 sites (fig. S9B). Furthermore, OTX2 as well as NANOG were also strongly enriched at the OCT4$^{EpiLC}$ sites in FA-RAS$^{KO}$ ESC, suggesting that, besides OCT4, OTX2 might also relocate additional naïve pluripotent factors (if expressed) to these sites prior to full differentiation (Fig. 6D and fig. S9B). Finally, we examined whether OTX2 and NANOG enrichment correlated with increased expression of post-implantation epiblast genes associated with ERF/OCT4$^{Common}$ sites in FA-RAS$^{KO}$ ESC. We found genes showing a similar level of expression in FA-RAS$^{KO}$ ESC compared to FA-RAS$^{lox/lox}$ (Fig. 6E, and fig. S9C). Our data demonstrate that FA-RAS$^{KO}$ ESC show promiscuous OTX2 and NANOG binding at OCT4$^{ESC}$ sites and OCT4$^{EpiLC}$ sites, which correlates with the expression of both naïve and primed markers in preparation for the transition towards primed pluripotency.

**ERF controls the expression of LIN28 proteins**

We next investigated how ERF controls the exit from the developmental blockage of RAS-deficient cells by mining our RNAseq data (Fig. 3). Interestingly, almost 20% of all differentially expressed genes identified in 2iL-ERF$^{KO}$ compared to 2iL-RAS$^{lox/lox}$ ESC are associated by proximity

to ERF peaks and mostly overlapping ESC enhancers (Supplementary Data S8). By combining differential gene expression between our different genetic conditions and differentiation status together with nearby ERF binding occupancy, we identified LIN28A and B as putative regulators. Expression of LIN28A/B is low in 2iL-ESC but is upregulated by FGF signaling during the transition to primed pluripotency. Of note, LIN28A and/or LIN28B-deficient ESC showed impaired conversion into EpiLC, revealing a critical role for these proteins in regulating the exit from naïve pluripotency (*29*). Induction of EpiLC differentiation in $RAS^{lox/lox}$ and $ERF^{KO}$ ESC demonstrated efficient LIN28s upregulation while FA-$RAS^{KO}$ ESC showed low or negligible levels of LIN28A and LIN28B, respectively (Fig. 7A and Supplementary Data S9). ERF deficiency restored the levels of LIN28 proteins in FA-$RAS^{KO}$; $ERF^{KO}$ (Fig. 7A). Interestingly, 2iL-$ERF^{KO}$ ESC showed already elevated levels of LIN28 proteins before differentiation, suggesting that ERF mediates a direct negative regulation on these genes. Indeed, we found ERF bound to an enhancer region in the second intron of LIN28 proteins in $RAS^{KO}$ ESC (Fig. 7B, and fig. S10A). Moreover, transition to EpiLC correlated with increased levels of H3K27ac at the LIN28 enhancers, and thus, LIN28 expression (Fig. 7B).

LIN28 proteins are RNA binding proteins known for binding to and inactivating the let-7 microRNA family. Functionally, let-7 microRNAs target a number of mRNA transcripts for degradation including MYC, RAS, HMGA2 and the two *de novo* methyltransferases DNMT3A and DNMT3B (*30*). Indeed, naïve ESC exhibit low levels of genome wide CpG methylation, which increase during the transition to EpiLC, correlating with the silencing of the naïve transcriptional program (31, 32). Accordingly, induction of $RAS^{lox/lox}$ and $ERF^{KO}$ ESC into EpiLC by FA demonstrated efficient upregulation of DNMT3 proteins while FA-$RAS^{KO}$ ESC showed low levels of DNMT3B (Fig. 7A). As expected, expression of DNMT3 proteins was efficiently rescued in FA-$RAS^{KO}$; $ERF^{KO}$ (Fig. 7A). We next examined the levels of 5-methylcytosine (5mC) by dot blot in all different genotypes, $RAS^{lox/lox}$, $ERF^{KO}$, $RAS^{KO}$, and $RAS^{KO}$; $ERF^{KO}$, grown under naïve or primed conditions (fig. S10B). The low levels of 5mC detected in 2iL rapidly increased upon FA treatment in $RAS^{lox/lox}$, $ERF^{KO}$ and $RAS^{KO}$; $ERF^{KO}$ ESC. However, FA-$RAS^{KO}$ ESC remained largely hypomethylated (fig. S10B). To gain further insights into methylation dynamics on a genome-wide manner, we performed reduced representation bisulfite sequencing (RRBS) in all genotypes and pluripotent states (Fig. 7, C and

D) (*33*). 2iL-RAS$^{lox/lox}$ ESC presented low levels of methylation (6.55% of analyzed CpG sites are methylated), which were increased after differentiation (21.75%). Furthermore, 2iL-ERF$^{KO}$ ESC showed higher average methylation levels in 2iL (12.1%) and FA (24.7%) conditions, consistent with their bias toward differentiation and their less optimal naïve transcriptional network (Fig. 7C, D). Conversely, RAS$^{KO}$ ESC showed extremely low methylation levels in 2iL conditions (1.55%) reaching similar levels to those found in 2iL-RAS$^{lox/lox}$ ESC when differentiated (6.9%) (Fig. 7, C and D). As expected, the defect in methylation observed in RAS$^{KO}$ ESC was rescued upon ERF deletion (Fig. 7, C and D). Interestingly, ERF$^{KO}$ ESC showed higher levels of methylation around transcription start sites as well as in CpG islands (Fig. 7E), especially after differentiation. Finally, we examined whether expression of DNMT3B could rescue the developmental trapping of FA-RAS$^{KO}$ ESC. However, our results showed that DNMT3B expression is not sufficient to overcome RAS deficiency and phenocopy ERF deficiency. This suggests that decommission of naïve enhancers and super-enhancers is required in FA-RAS$^{KO}$ ESC for the transition to primed pluripotency and needs to occur prior to DNMT3B-mediated DNA methylation (fig. S10, C and D). Collectively, our data showed that ERF regulates negatively the expression of LIN28 and DNMT3 proteins and timely coordinates their expression during naïve to primed transition. The altered expression of these proteins might underlie the global disbalance in the methylation levels at a genome-wide scale in ERF-deficient cells.

## DISCUSSION

Preceding implantation, the cells residing within the naïve ICM of the blastocyst transition through a distinct phase of primed pluripotency in preparation for lineage commitment. This transition is initiated by fibroblast growth factor 4 (FGF4)-dependent activation of the RAS/MAPK pathway (*34, 35*). Despite the relevance of the MAPK pathway during this critical period, little is known about how RAS proteins instruct this transition. Here, we used RAS-deficient ESC for a careful dissection of the FGF pathway and demonstrated that the transcriptional factor ERF is the sole MAPK-dependent switch that controls the naïve-to-primed transition.

FA-RAS$^{KO}$ ESC are characterized by an active naïve transcriptional network, high expression of OTX2 and elevated expression of primed markers. This suggests that 1) activation of the primed transcriptional program does not require full exit from naïve pluripotency, and 2) FGF/MAPK is the main pathway controlling the exit from naïve pluripotency. Indeed, our data revealed that ERF imposes an exquisite level of coordination during the transition from naïve to primed pluripotency. In the absence of MAPK signaling, chromatin bound ERF ensures elevated expression of naïve pluripotent factors, including NANOG (Fig. 4). High levels of NANOG maintain the undifferentiated state of ESC in the absence of LIF and might shield naïve embryonic cells from premature commitment (*26, 36*). Accordingly, ERF$^{KO}$ ESC showed decreased levels of NANOG and undergo a partial exit from naïve pluripotency under 2iL conditions (Fig. 4). Our data suggest that ERF safeguards naïve pluripotency in the absence of MAPK signaling, at least partially, by sustaining elevated levels of NANOG. It seems counter-intuitive to find ERF, a transcriptional repressor, bound to enhancers and super-enhancers controlling the expression of highly naïve transcribed genes. Interestingly, it has been recently shown that addition of CDK8/19 inhibitors (CDK8/19i) to FBS/LIF growing ESC promotes enhancer hyperactivation and stabilizes the naïve state by facilitating Mediator activity as efficiently as in the 2i condition (*37*). This effect seems to be independent of the MAPK pathway as the use of CDK8/19i eliminates the ability of the CDK8 module to repress the activity of the Mediator complex at enhancers. Accordingly, CDK8/19i-ESC showed phosphorylated cytoplasmic ERF (*38*), suggesting that the use of CDK8/19i can bypass the need of nuclear ERF to promote the naïve transcriptional program. Future work will be necessary to determine whether ERF bound in active enhancers could restrict the

recruitment of the CDK8 module facilitating Mediator activity. In fact, other ETS transcription factors such as ELK1 can interact directly with Mediator in a ERK phosphorylation-dependent manner (*39*).

ERF also controls negatively the expression of LIN28 proteins as 2iL-ERF$^{KO}$ ESC showed increased levels of both LIN28A and B. Although LIN28 proteins regulate the expression of DNMT3 proteins by sequestering let-7 microRNAs, we did not detect upregulation of the methyltransferases in naïve ERF$^{KO}$ ESC (Fig. 7). This is likely due to high levels of PRDM14, which represses expression of DNMT3 methyltransferases by recruiting Polycomb repressive complex 2 to their promoters, and it is regulated by ERF (Fig. 5E) (*40*). Thus, coordinated PRDM14 downregulation and increased LIN28 expression through ERF-dependent mechanisms could contribute to DNMT3 upregulation and increased methylation during the transition to primed pluripotency. Although DNMT3A and DNMT3B are dispensable for a successful exit from naïve pluripotency, *de novo* DNA methylation facilitates a timely progression towards a primed state (*41*). In fact, DNMT3A/B double knockout ESC exhibited a delayed exit from the naïve state and defective expression of the post-implantation markers OCT6, FGF5 or OTX2 (*41*). This is ultimately due to persistent NANOG expression after 2iL withdrawal as DNMT3A/B deficiency leads to reduced CpG methylation at the proximal NANOG promoter (*41, 42*). Similarly, FA-RAS$^{KO}$ ESC showed negligible expression of DNMT3B and, therefore, high levels of NANOG. Interestingly, ERF$^{KO}$ ESC showed increased DNA methylation compared to RAS$^{lox/lox}$ ESC and is particularly evident in genes and CpG islands after the transition to EpiLC (Fig. 7E). Naïve ERF$^{KO}$ ESC have low levels of DNMT3 expression but elevated levels of DNMT3L, the catalytically inactive regulatory factor of *de novo* DNA methyltransferases (fig. S10C), which can contribute to this bias during differentiation (*43*). Furthermore, DPPA3, also known as Stella and implicated in preventing excessive DNA methylation by sequestering the E3 ubiquitin ligase UHRF1, is also decreased in ERF$^{KO}$ ESC (Fig. S10E) (*44*). Importantly, downregulation of DPPA3 mediated by DNMT3 methylation has been shown to be a key event in the naïve to primed conversion (*45*). Collectively, elevated levels of DNMT3L and low levels of DPPA3 in naïve conditions could contribute to the aberrant level of methylation detected in FA-ERF$^{KO}$. Nevertheless, these changes in methylation do not result in major transcriptional changes in FA-ERF$^{KO}$ compared to their respective control cells.

FA-RAS$^{KO}$ ESC showed high but heterogenous expression of OTX2, which has been shown a critical transcription factor for the maintenance of intermediate states of pluripotency (*7-10*). The consequence of having high levels of OTX2 in this context can be inferred by previous studies (*27*). Indeed, OTX2 over-expression has been shown to redirect OCT4 to previously inaccessible sites in EpiLC, decrease expression of naïve markers (TBX3 or ESRRB), and induce EpiLC genes, such as FGF5 (*27*). Interestingly, these effects take place in the presence of MEKi, a situation that is mirrored in FA-RAS$^{KO}$ ESC. The ability of OTX2 to engage new enhancer sequences not only depends on its levels but also on the cooperative help of additional transcription factors (*27*). This cooperation might explain the enrichment of OTX2 in active naïve enhancers in FA-RAS$^{KO}$ ESC. Moreover, our data also showed that, in addition to OCT4, NANOG is mobilized to sites that become active in EpiLC, which results in partial or full transcriptional activation (Fig. 6E). In this context, NANOG relocation might facilitate OTX2 positioning as it has been shown to promote chromatin accessibility and TF recruitment together with BRG1, part of the large remodeling complex SWI/SNF (*26*).

Finally, we showed that FA-RAS$^{KO}$ ESC can be maintained in culture under primed conditions and could be a suitable genetic model to study intermediate states of pluripotency. Indeed, FA-RAS$^{KO}$ ESC mirrored transcriptionally cells that have departed 12-24 hours from naïve pluripotency and are reminiscent of the recently described pluripotent intermediate states (*7-10*). Future studies will be necessary to determine the similarity of all these intermediate states with corresponding *in vivo* counterparts and the origin of the intrinsic heterogeneity observed in FA-RAS$^{KO}$ ESC. Nevertheless, pluripotency can be considered as a dynamic property associated to different transient stem cell states that can be recapitulated by using different inhibitors and/or growth factors. By using RAS$^{KO}$ ESC we focused specifically on the FGF pathway and the role of RAS proteins during the naïve to primed transition.

Future studies will be needed to determine if ERF plays a role in other cell fate decisions during early embryonic development such as in primitive endoderm specification, where FGF4-dependent activation of the MAPK pathway is also necessary. Moreover, the control of ERF over PRDM14 expression suggested that ERF might also play an important role in germline fate (*46*).

In conclusion, here we demonstrated the essential role of ERF as regulator of the timely transition to primed pluripotency.

## MATERIALS AND METHODS

### Embryo Culture

All the animal work included here was performed in C57BL/6J mice obtained from the Jackson Laboratory in compliance with the NIH Animal Care & Use Committee (ACUC) Guideline for Breeding and Weaning. Following procedures previously described in (*48*), 4-weeks old female mice were injected intraperitoneally with 5IU Pregnant Mare Serum Gonadotropin (PMSG, Prospec) followed by 5 IU human Chorionic Gonadotropin (hCG, Sigma-Aldrich) 46-48 hours later. Alternatively, 8-weeks naturally pregnant females were euthanized, and embryos collected in M2 media (MR-015-D, Sigma-Aldrich) at indicated time points after hCG injection: E2.75, E3.5, E4.0, E4.75. The sex of embryos was not determined. Embryos were fixed in 4% Paraformaldehyde (Electron Microscopy Sciences) for 10 min, permeabilized for 30 min in 0.3% Triton X-100 and 0.1M Glycine in PBS 1X and blocked for 1 hour (1% BSA, 0.1% Tween in PBS 1X). Embryos were incubated overnight with primary antibodies (see Table S2), washed in 0.1% Tween in PBS 1X and incubated with the secondary antibody accordingly for 1 hour at room temperature. Embryos were imaged using a Nikon Ti2-E microscope (Nikon Instruments) equipped with a CSU-W1 spinning disk (Yokogawa), Photometrics Prime BSI sCMOS (Photometrics), and 60x Nikon Apochromat TIRF objective (NA = 1.49). Z-stacks were acquired with a x-y pixel size of 0.11 mm and z-step of 0.9 mm. For quantification, embryo z-stack images were quantified using Imaris Bitplane (Oxford Instruments). 3D surfaces were rendered based on nuclear DAPI-staining and the corresponding regions were used to quantify the fluorescence intensity of ERF, NANOG, and KLF4. For experiment shown in Fig. 1B shows one representative experiment with the following embryos and cells used for quantification: Exp 1: E2.75: 3 Embryos, 24 cells in total. E3.5: 3 Embryos, 117 cells total, E4.0: 4 Embryos, 168 cells total, E4.75: 1 Embryo: 75 cells. Exp 2: E3.5: 8 embryos, E3.75: 4 embryos, E4.0: 6 embryos.

### Cell culture and differentiation

N-*Ras*$^{-/-}$; H-*Ras*$^{-/-}$; K-*Ras*$^{f/f}$; *Ubiq-Cre*$^{ERT2}$ (RAS$^{lox/lox}$) (*17*) ESC were grown in N2B27 media supplemented with 2i/LIF (1 mM PD0325901, 3 mM CHIR99021, both from Tocris and 1:500 LIF,

made in house). N2B27 media consisted of a 1:1 mix of DMEM/F12 and Neurobasal Medium, 1X N2 supplement, 1X B27 supplement, 0.1 mM nonessential amino acids, 55 μM β-mercaptoethanol and 1% penicillin/streptomycin (all from Life Technologies). Cells were routinely cultured in 0.1% gelatinized plates and passaged with Accutase (Gibco) unless otherwise indicated. To induce EpiLC differentiation, cells were grown for few passages in plates pretreated with 10 μg/ml polyL-ornithine and 5 μg/ml laminin (Corning). A total of 200,000–300,000 cells per 10 $cm^2$ were plated on plates pretreated with 5 μg/ml Fibronectin (Millipore) in N2B27 media supplemented with 1% KOSR, 12 ng/ml FGF2 (R&D systems) and 20 ng/ml Activin A (PeproTech) for 48 hours including daily media changes. For inducing CRE-mediated deletion of K-RAS allele, we incubated $RAS^{lox/lox}$ ESC with 1μM 4-hydroxytamoxifen (4-OHT, Sigma-Aldrich) for 6 days before performing any experiment. To maintain EpiLC in culture, ESCs were plated in N2B27 media with 12 ng/ml FGF2, 20 ng/ml Activin A and 1 mM XAV939 on Fibronectin-coated plates at a density of 10,000 cells per $cm^2$. EpiLC were passaged the first time with Accutase including 1 mM Y27632 to enhance plating efficiency. Media was changed every other day and passaged every 2-3 days. HEK293T (American Type Culture Collection) cells were grown in DMEM, 10% FBS, and 1% penicillin/streptomycin.

To generate ESC lines carrying a DOX-inducible DNMT3B-PiggyBac construct, the coding sequence for DNMT3B was amplified from cDNA and subcloned into the plasmid PB-TRE-dCas9-VPR (Gift from George Church, 63800, Addgene), after removing the dCas9-VPR insert. DOX-inducible PiggyBac-DNMT3B plasmid together with a plasmid encoding for a supertransposase were co-transfected in ESC and selected with Hygromycin (200ug/ml) for one week.

To target a short half-life form of eGFP (deGFP) in the endogenous REX1 gene, we generated a targeting vector by inserting deGFP in pCR®-Blunt II TOPO® (Zero Blunt TOPO PCR cloning kit, Invitrogen). Homology arms PCR-amplified from endogenous sequences upstream of the start codon and downstream of the stop codon from REX1 were cloned to flank pCR®-Blunt II TOPO®-deGFP. In addition, specific small guide RNA (sgRNA) sequences targeting the surroundings of the REX1 start codon were cloned into the plasmid pX330-U6-Chimeric_BB-CBh-hSpCas9 (Gift from Feng Zhang, 42230, Addgene) (*49*). The sequences of the sgRNAs were designed with the Genetic Perturbation Platform sgRNA designer tool

(https://portals.broadinstitute.org/gpp/public/analysis-tools/sgrna-design). Both plasmids were transfected in ESC using Jetprime (Polyplus transfection) to induce the targeting and cell sorted based on GFP intensity to isolate individual clonal ESC lines. See Table S1 for primer information.

**Clonogenicity Assay**

ESC were withdrawn of 2i/LIF for 48 hours and plated at single cell density (50 cells/$cm^2$) in N2B27 media with 2i/LIF on plates coated with 0.1% gelatin (Sigma). At day 5, alkaline phosphatase staining was performed using the Alkaline Phosphatase Detection Kit (Millipore). Colonies were counted manually. At least three independent experiments with three replicates per experiment were performed.

**Generation of self-organizing embryonic spheres**

ESC growing on gelatinized plates in N2B27 media with 2i/LIF were dissociated with Accutase and washed with PBS before their resuspension in growth factor reduced Matrigel (Corning) at a concentration of 10,000 cells/20μl of matrigel. The suspension was deposited in drops in 8-μwell Ibidi microplates and incubated at 37°C until the Matrigel solidified. Wells were then filled with N2B27 media without 2i/LIF and cultured for 48-72 hours at 37°C and 5% CO2. To inhibit WNT signaling, embryonic spheres were incubated with 2μM IWR-1 for the duration of the assay. ESC-derived spheres were fixed in 4% PBS–paraformaldehyde (PFA) for 10 min at room temperature. Permeabilization was performed in PBS containing 0.3% Triton X-100 (Sigma) and 0.1 M glycine (Sigma) for 30 minutes at room temperature. Spheres were incubated with primary antibodies at 4°C overnight, followed by incubation with corresponding fluorescently conjugated Alexa Fluor secondary antibodies for 2 hours at room temperature. Both primary and secondary antibodies were diluted in PBS containing 1% BSA (Sigma) and 0.1% Tween20 (Sigma). See Table S2 for antibody information.

**Western blot**

Following procedures previously described in (*48*) cells were lysed in 50 mM Tris pH 8, 8 M Urea (Sigma) and 1% Chaps (Millipore) followed by 30 min of shaking at 4°C. 20 μg of supernatants

were run on 4%-12% NuPage Bis-Tris Gel (Invitrogen) and transferred onto Nitrocellulose Blotting Membrane (GE Healthcare). Membranes were blocked in 5% skim milk (Millipore) and 0.1% Tween 20 (Sigma) in PBS. Membranes were incubated with the primary antibody overnight at 4°C (see Table S2), followed by incubation with HRP-conjugated secondary antibodies (1:5000) for 1 h at room temperature (*48*). Membranes were developed using SuperSignal West Pico PLUS (Thermo Scientific). See Table S2 for antibody information. Quantification was performed by using Image Lab 6.0.1 (BioRad).

**Dot blot**

Trypsinized ESC were lysed for 2-3 hours at 55°C with lysis buffer (100 mM Tris-HCl pH 8, 5 mM EDTA, 0.2% SDS, 20 mM NaCl and 100 μg/ml Proteinase K). DNA was isolated by adding an equal volume of Phenol/Chloroform/Isoamyl to the samples and using phase-lock tubes (5PRIME Phase Lock Gel™ Heavy, Quantabio), followed by an extraction with identical volume of Chloroform. DNA was precipitated with 2 volumes of 100% Ethanol plus 0.3 M NaAc, washed with 70% Ethanol and resuspended in water. A total of 500 ng of DNA was diluted in 0.3 M NaOH and denatured at 42°C for 12 minutes. After incubation, the samples were rapidly transferred by spotting each sample into a nitrocellulose membrane (Nitrocellulose Blotting Membrane, GE Healthcare). After the transfer, DNA was crosslinked with a Stratalinker® UV crosslinker (Stratagene) using the Autocrosslink setting. The membrane was blocked in 5% skim milk (Millipore) and 0.1% Tween 20 (Sigma) in PBS, incubated with 1:500 dilution of the anti-5mC antibody (see Table S2) overnight at 4°C, followed by incubation with HRP-conjugated secondary antibody (1:5000) for 1 h at room temperature. Membrane was developed using SuperSignal West Pico PLUS (Thermo Scientific). See Table S2 for antibody information.

**Flow cytometry**

For flow cytometry experiments, cells were dissociated into single cell suspensions and analyzed for GFP gene expression using a FACS Fortessa (BD Biosciences). DAPI was added to detect cells with compromised membrane integrity. Data was analyzed using FlowJo. At least two independent experiments were performed.

**High throughput imaging (HTI)**

Following procedures previously described in (*48*), a total of 10,000-20,000 ESC were plated in 2i/LIF conditions on gelatin or 5 μg/ml Fibronectin (Millipore) in μCLEAR bottom 96-well plates (Greiner Bio-One, 655087). ESC were either maintained in 2i/LIF conditions or treated with FGF2/ActA for the indicated times. Staining was performed using standard procedures. DNA was stained using DAPI (4',6-diamidino-2-phenylindole).

Images were automatically acquired using a CellVoyager CV7000 high throughput spinning disk confocal microscope (Yokogawa, Japan). Each condition was performed in triplicate wells and/or at least 9 different fields of view (FOV) were acquired per well. High-Content Image (HCI) analysis was performed using the Columbus software (PerkinElmer). In brief, nuclei were first segmented using the DAPI channel. Mean fluorescence intensities for OTX2, ERF, ESRRB or NANOG signal were calculated over the nuclear masks in their respective channels. Single cell data obtained from the Columbus software was exported as flat tabular .txt files, and then analyzed using RStudio version 1.2.5001, and plotted using Graphpad Prism version 9.0.0 (*48*).

**Immunofluorescence**

Cells were fixed in 4 % Paraformaldehyde (Electron Microscopy Sciences) for 10 min at room temperature, permeabilized in 100 mM Tris-HCl pH 7.4, 50 mM EDTA pH 8.0, 0.5% Triton X-100 and incubated with the corresponding primary antibodies overnight (see Table S2). This was followed by incubation with corresponding fluorescently conjugated Alexa Fluor secondary antibodies for 2 h at room temperature. Both primary and secondary antibodies were diluted in PBS containing 1% BSA (Sigma) and 0.1% Tween20 (Sigma). Images were acquired using either a Nikon spinning disk confocal microscope (CSU-W1) or a Zeiss LSM880 Airyscan microscope. See Table S2 for antibody information.

**RNAseq and data analysis**

RNA was isolated using the ISOLATE II RNA Mini Kit (Bioline) following manufacturer's recommendations. DNA libraries for RNAseq analysis were prepared using NEBNext Ultra II

Directional RNA Library Prep Kit for Illumina (New England Biolabs, NEB) and NEBNext rRNA Depletion Kit (Human/Mouse/Rat) (NEB) according to the manufacturer's protocol. Sequencing was performed on the Illumina NextSeq550 (75bp pair-end reads). RNAseq reads were adapter trimmed using fastp v.0.20.0 (*50*). Transcript expression was quantified via mapping to mouse gencode v25 transcripts using salmon (*51*). Identification of differentially expressed genes between samples was performed using DESEQ2 (*52*). RNAseq coverage tracks were generated by aligning RNAseq reads to UCSC version mm10 of the mouse genome using the STAR v2.6.1a aligner (*53*) followed by application of the 'bamCoverage' utility from deeptools (*54*) to generate signal track files with the following parameters: normalization=RPKM, bin_size=50, smooth_length=1. For comparison to other published RNAseq data sets, gene counts across samples were quantile-normalized using the limma package (*55*). Batch correction was then performed on quantile-normalized counts using COMBAT (*56*). See Table S3 for further software and algorithm information.

**CUT&RUN protocol**

The CUT&RUN protocol was slightly modified from (*57, 58*). Following procedures previously described in (*48*), cells were washed twice with Wash Buffer (20 mM HEPES-KOH pH 7.5, 150 mM NaCl, 0.5 mM spermidine, Roche complete Protease Inhibitor tablet EDTA free) and bound to activated Concanavalin A beads (Polysciences) for 10 minutes at room temperature. Cells were then permeabilized in Digitonin Buffer (0.05 % Digitonin and 0.1% BSA in Wash Buffer) and incubated with corresponding antibodies at 4°C for 2 hours. For negative controls, Guinea Pig anti-Rabbit IgG (Antibodies-online) was used. Following antibody incubation, cells were washed with Digitonin Buffer and incubated with a hybrid protein A-protein G-Micrococcal nuclease (pAG-MNase) at 4°C for 1 hour. Samples were washed in Digitonin Buffer, resuspended in 150 µl Digitonin Buffer and equilibrated to 0°C on ice water for 5 minutes. To initiate MNase cleavage, 3 µl 100 mM $CaCl_2$ was added to cells and after 1 hour of digestion, reactions were stopped with the addition of 150 µl 2x Stop Buffer (340 mM NaCl, 20 mM EDTA, 4 mM EGTA, 0.02 % Digitonin, 50 µg/ml RNase A, 50 µg/ml Glycogen). Samples were incubated at 37°C for 10 minutes to release DNA fragments and centrifuged at 16,000 g for 5 minutes. Supernatants were collected

and a mix of 1.5 µl 20% SDS / 2.25 µl 20 mg/ml Proteinase K was added to each sample and incubated at 65°C for 35 minutes. DNA was precipitated with ethanol and sodium acetate and pelleted by high-speed centrifugation at 4°C, washed, air-dried and resuspended in 10 µ 0.1x TE. See Table S2 for antibody information.

**Library preparation and sequencing**

Following procedures previously described in (*48*), the entire precipitated DNA obtained from CUT&RUN was used to prepare Illumina compatible sequencing libraries. In brief, end-repair was performed in 50 µl of T4 ligase reaction buffer, 0.4 mM dNTPs, 3 U of T4 DNA polymerase (NEB), 9 U of T4 Polynucleotide Kinase (NEB) and 1 U of Klenow fragment (NEB) at 20°C for 30 minutes. End-repair reaction was cleaned using AMPure XP beads (Beckman Coulter) and eluted in 16.5 µl of Elution Buffer (10 mM Tris-HCl pH 8.5) followed by A-tailing reaction in 20 µl of dA-Tailing reaction buffer (NEB) with 2.5 U of Klenow fragment exo- (NEB) at 37°C for 30 minutes. The 20 µl of the A-tailing reaction were mixed with Quick Ligase buffer 2X (NEB), 3000 U of Quick Ligase (NEB) and 10 nM of annealed adaptor (Illumina truncated adaptor) in a volume of 50 µl and incubated at room temperature for 20 min. The adaptor was prepared by annealing the following HPLC-purified oligos: 5'-Phos/GATCGGAAGAGCACACGTCT-3' and 5'-ACACTCTTTCCCTACACGACGCTCTTCCGATC*T-3' (*phosphorothioate bond). Ligation was stopped by adding 50 mM of EDTA, cleaned with AMPure XP beads and eluted in 14 µl of Elution Buffer. All volume was used for PCR amplification in a 50 µl reaction with 1 µM primers TruSeq barcoded primer p7, 5'-CAAGCAGAAGACGGCATACGAGATXXXXXXXXGTGACTGGAGTTCAGACGTGTGCTCTTCCGATC*T-3' and TruSeq barcoded primer p5 5'-AATGATACGGCGACCACCGAGATCTACACXXXXXXXXACACTCTTTCCCTACACGACGCTCTTCCGATC*T-3' (* represents a phosphothiorate bond and XXXXXXXX a barcode index sequence), and 2X Kapa HiFi HotStart Ready mix (Kapa Biosciences). The temperature settings during the PCR amplification were 45 s at 98°C followed by 15 cycles of 15 s at 98°C, 30 s at 63°C, 30 s at 72°C and a final 5 min extension at 72°C. PCR reactions were cleaned with AMPure XP beads (Beckman Coulter), run on a 2% agarose gel and a band of 300bp approximately was cut and gel purified

using QIAquick Gel Extraction Kit (QIAGEN). Library concentration was determined with KAPA Library Quantification Kit for Illumina Platforms (Kapa Biosystems). Sequencing was performed on the Illumina NextSeq550 (75bp pair-end reads).

**Cut&Run data processing**

Data were processed using a modified version of Cut&RunTools (*59*). Reads were adapter trimmed using fastp v.0.20.0 (*50*). An additional trimming step was performed to remove up to 6bp adapter from each read. Next, reads were aligned to the mm10 genome using bowtie2 (*60*) with the 'dovetail' and 'sensitive' settings enabled. Normalized (RPKM) signal tracks were generated using the 'bamCoverage' utility from deepTools with parameters bin-size=25, smooth length=75, and 'center_reads' and 'extend_reads' options enabled (*48*, *54*). See Table S3 for further software and algorithm information.

**Processing for published ChIP datasets**

External next generation sequencing data were downloaded from the Sequence Read Archive (SRA) and analyzed as follows. These analyses include a re-analysis of our original datasets (*11*). Reads were aligned to the mm10 genome using bowtie2 (*60*). Duplicate reads were removed using MarkDuplicates from the Picard toolkit (http://broadinstitute.github.io/picard/). Normalized (RPKM) signal tracks were generated bamCoverage utility from deepTools (*54*), using the parameters bin-size=25, smooth length=75, 'center_reads' and 'extend_reads'. For paired-end data, read mates were extended to the fragment size defined by the two read mates. For single-end ChIP-seq data, reads were extended to the estimated fragment length estimated by phantompeakqualtools (*61*). See Table S3 for further software and algorithm information.

**Identification of OCT4 binding sites in ESC and EpiLC**

Fastq files from published OCT4 ChIP-seq data for ESC (SRR1202455, SRR1202456), EpiLC plus and minus Activin-A (SRR1202468, SRR1202469), and associated input controls (SRR1202465, SRR1202464, SRR1202477 SRR1202478) (*27*) were downloaded from the Sequence Read Archive (SRA). Single-end reads were aligned to the mm10 genome using bwa (*62*). Duplicate reads were removed using MarkDuplicates from the Picard toolkit (http://broadinstitute.github.io/picard/),

and peaks for each sample were called using macs2 (*63*) with q-value cutoff < 0.01 and extension length determined using phantompeakqualtools (*61*). Diffbind (*64*) using the DeSeq2 method was used to determine differentially bound peaks, treating EpiLC plus and minus Activin-A samples as replicate experiments as was done in the original study (*27*). Peaks were determined to be ESC- or EpiLC-specific if they differed by 2-fold read concentration with p-val<0.01 and FDR <0.03. A subset of peaks with > mean read concentration for EpiLC and ESC with <0.5 fold difference were selected as "common" or shared peaks. See Table S3 for further software and algorithm information.

**RRBS data processing**

DNA libraries for RRBS analysis were prepared using the Premium RRBS kit (Diagenode) following manufacturer's recommendations. Sequencing was performed on the Illumina NextSeq550 (75bp single-end reads). Single-end RRBS reads were adapter and quality trimmed (phred33 score>=20) using trimgalore v0.6.5 (http://www.bioinformatics.babraham.ac.uk/projects/trim_galore) with the RRBS option invoked. Bismark v0.22.1 (*65*) was used to align reads to UCSC version mm10 of the mouse genome. CpG methylation was extracted using bismark ignoring the first 4 bases of the read after inspection of m-bias plots. Methylation summary statistics were computed using the methylKit package (*66*). See Table S3 for further software and algorithm information.

**Quantification and statistical analysis.**

All information regarding statistical details of the experiments, number of experiments, statistical tests used, number of cells/experiments can be found in the corresponding figure legends o methods section.

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**Author contributions:** M.V-S. and S.R. conceived the study. M.V-S., T.O., designed and performed experiments. C.N.D. and M.F. provided technical support. D.T. and P.C.F. analyzed sequencing data. A.D.T. and M.J.K. analyzed confocal microscopy data. S.R. supervised the study and wrote the manuscript with comments from all authors. **Competing interests:** The authors declare no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. The RNA-seq and Cut&Run data generated in this study have been deposited in the GEO database under accession GSE162581.

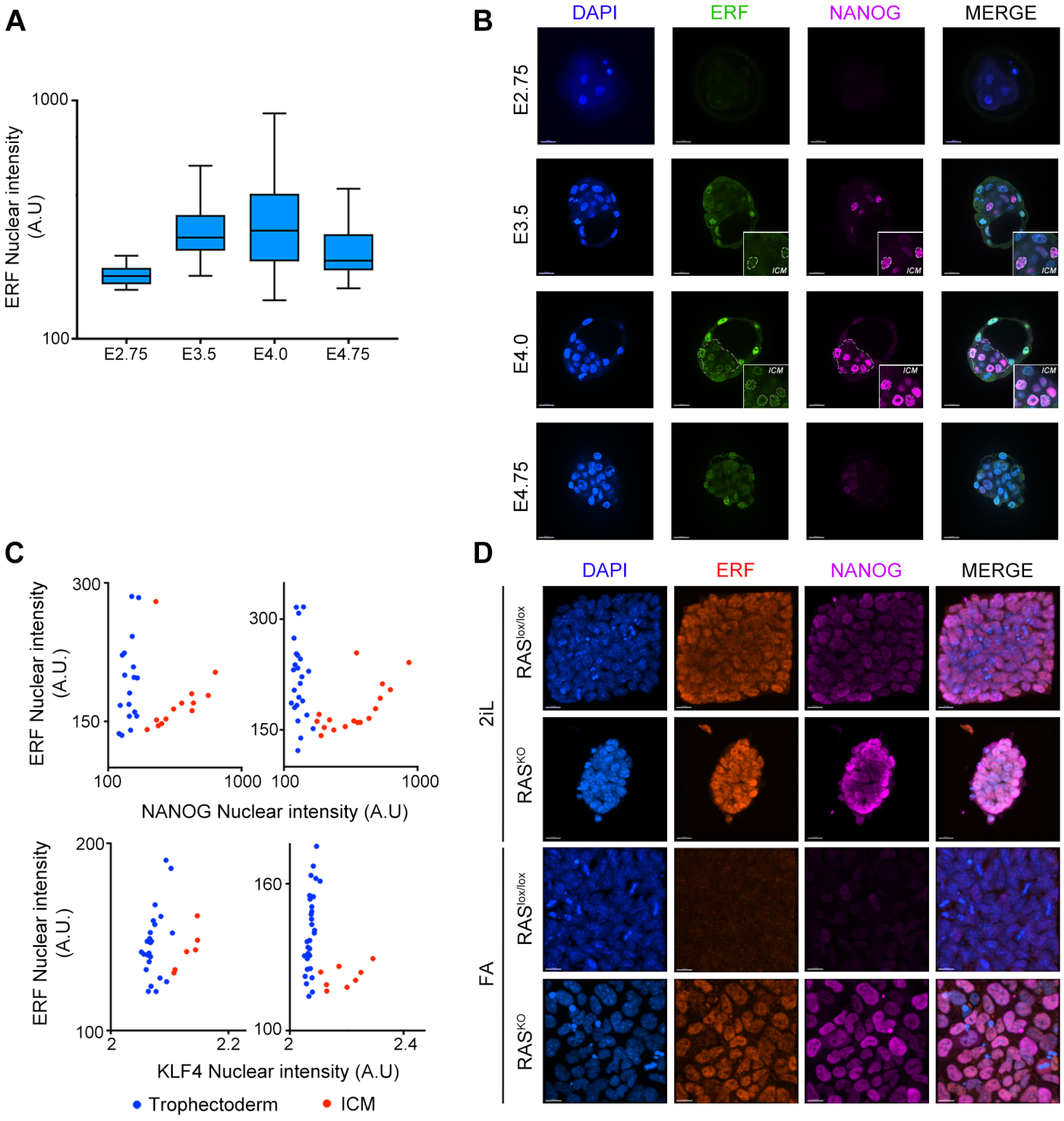
A
ERF Nuclear intensity (A.U)
1000
100
E2.75
E3.5
E4.0
E4.75
B
DAPI
ERF
NANOG
MERGE
E2.75
E3.5
E4.0
E4.75
ICM
C
ERF Nuclear intensity (A.U.)
300
150
100
1000
NANOG Nuclear intensity (A.U)
200
160
2
2.2
2.4
KLF4 Nuclear intensity (A.U)
Trophectoderm
ICM
D
DAPI
ERF
NANOG
MERGE
2iL
FA
RASlox/lox
RASKO

**Figure 1**

**FIGURE LEGENDS**

**Fig. 1. ERF expression correlates with naïve pluripotency markers.** (**A**) Graph showing mean nuclear fluorescent intensity for ERF in mouse embryos at different days of embryonic development (E). (**B**) Immunofluorescence analysis of NANOG and ERF in mouse embryos at E2.75, E3.5, E4.0 and E4.75. Note that ERF is expressed in both ICM and TE. However, at E4.75 ERF and NANOG are mostly downregulated in epiblast cells. Dashed line highlights the ICM. DAPI was used to visualize nuclei. Scale bars, 20μm. (**C**) Graphs showing relative nuclear fluorescence intensity of ERF and NANOG (upper plots) and ERF and KLF4 (lower plots). Every dot represents one single nucleus, and each plot corresponds to an individual E3.5 embryo. Two representative examples are shown but at least 10 embryos were analyzed. (**D**) Immunofluorescence analysis of 2iL and FA treated $RAS^{lox/lox}$ and $RAS^{KO}$ ESC and stained for ERF (red) and NANOG (purple). DAPI was used to visualize nuclei. Scale bars, 15μm.

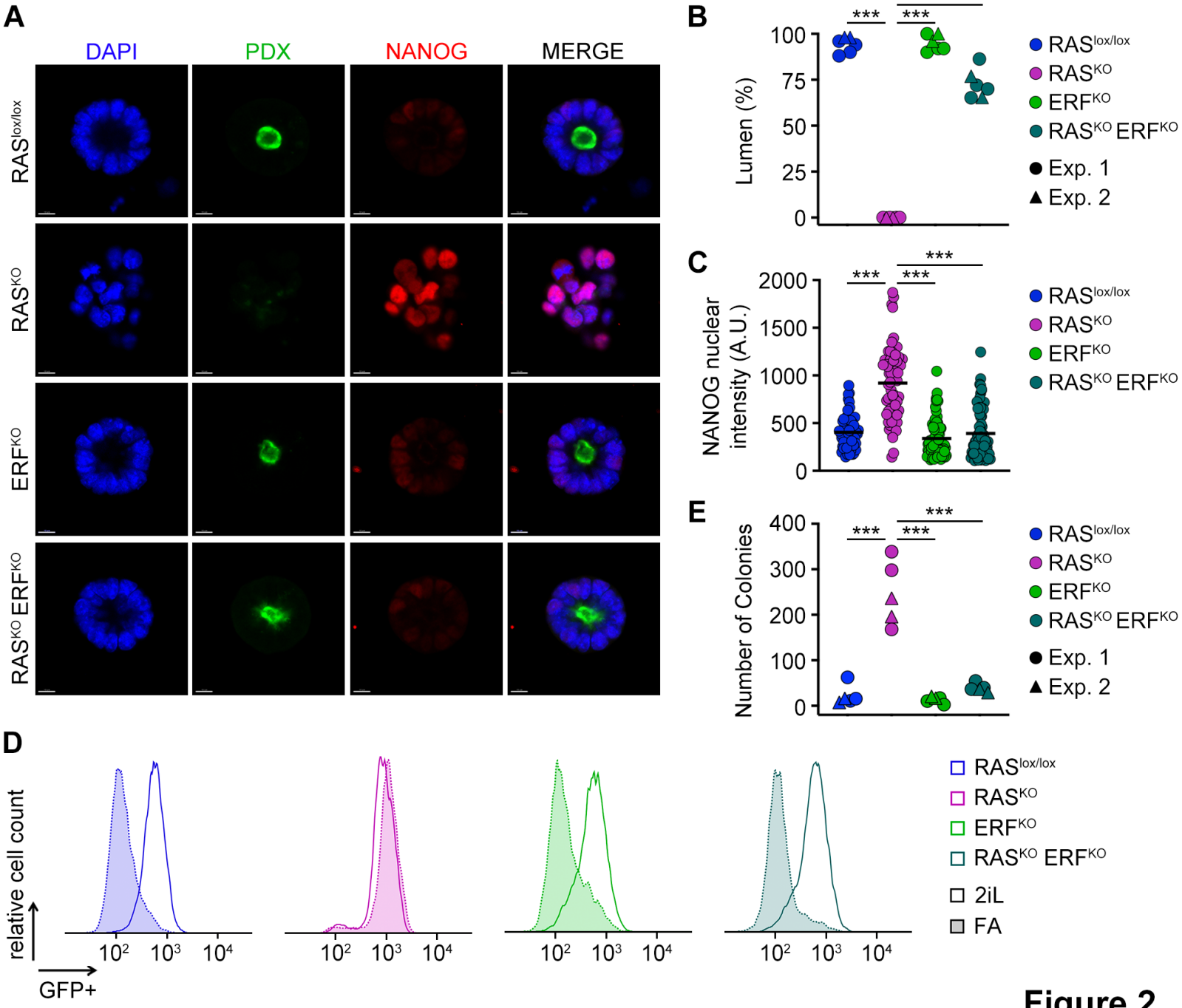
A
DAPI
PDX
NANOG
MERGE
RASlox/lox
RASKO
ERFKO
RASKO ERFKO
B
Lumen (%)
100
75
50
25
0
***
***
***
RASlox/lox
RASKO
ERFKO
RASKO ERFKO
Exp. 1
Exp. 2
C
NANOG nuclear intensity (A.U.)
2000
1500
1000
500
0
***
***
***
RASlox/lox
RASKO
ERFKO
RASKO ERFKO
E
Number of Colonies
400
300
200
100
0
***
***
***
RASlox/lox
RASKO
ERFKO
RASKO ERFKO
Exp. 1
Exp. 2
D
relative cell count
GFP+
10²
10³
10⁴
RASlox/lox
RASKO
ERFKO
RASKO ERFKO
2iL
FA

**Figure 2**

**Fig. 2. Successful exit from naïve pluripotency requires downregulation of ERF.** (**A**) Central confocal optical sections of $RAS^{lox/lox}$, $ERF^{KO}$, $RAS^{KO}$, and $RAS^{KO}$; $ERF^{KO}$ embryonic cell rosettes embedded in matrigel 48 hours after seeding and stained for NANOG (red) and podocalyxin (PDX; green). DAPI was used to visualize nuclei. Scale bars, 10μm. (**B**) Graph showing the percentage of embryonic rosettes generating a lumen (PDX+) in all genotypes. Two independent experiments are shown and at least, a total of 50 rosettes were counted per sample. ***=p<0.001. (**C**) Graph showing mean NANOG nuclear fluorescence intensity per nucleus in embryonic rosettes 48 hours after seeding. One representative experiment is shown and a total of 70 nuclei from different rosettes were counted per sample. ***=p<0.001. (**D**) Flow cytometry analysis of REX1-deGFP reporter ESC from all genotypes in 2iL-ESC and EpiLC after 48 hours of induction with FA. Three independent experiments were performed but one representative experiment is shown. (**E**) Graph showing the number of alkaline phosphatase positive colonies in a colony forming assay using ESC from all genotypes. Two independent experiments are shown with at least two technical replicates. ***=p<0.001.

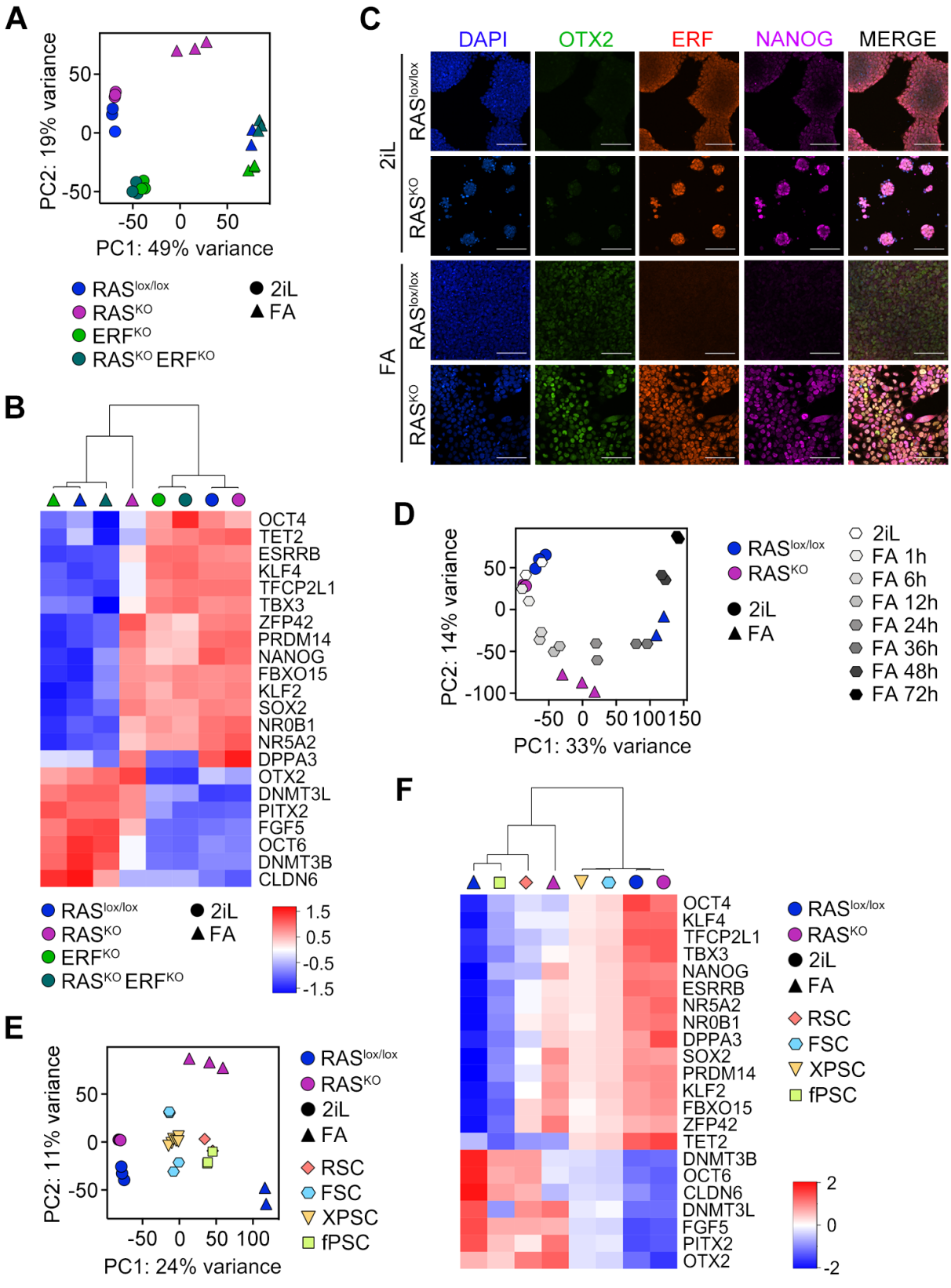
A
PC2: 19% variance
PC1: 49% variance
RASlox/lox
RASKO
ERFKO
RASKO ERFKO
2iL
FA
B
OCT4
TET2
ESRRB
KLF4
TFCP2L1
TBX3
ZFP42
PRDM14
NANOG
FBXO15
KLF2
SOX2
NR0B1
NR5A2
DPPA3
OTX2
DNMT3L
PITX2
FGF5
OCT6
DNMT3B
CLDN6
1.5
0.5
-0.5
-1.5
C
DAPI
OTX2
ERF
NANOG
MERGE
2iL
FA
D
PC2: 14% variance
PC1: 33% variance
2iL
FA 1h
FA 6h
FA 12h
FA 24h
FA 36h
FA 48h
FA 72h
E
PC2: 11% variance
PC1: 24% variance
RSC
FSC
XPSC
fPSC
F
2
0
-2

**Figure 3**

**Fig. 3. ERF controls the transition to primed pluripotency in a MAPK-depedent manner.** (**A**) PCA plot of RNAseq data of $RAS^{lox/lox}$, $ERF^{KO}$, $RAS^{KO}$, and $RAS^{KO}$; $ERF^{KO}$ ESC cultured in naïve conditions (2iL) or induced to differentiate to EpiLC (FA) for 48 hours. Three replicates per condition are shown. (**B**) Heatmap generated from RNAseq data from samples described in A) showing the average from three replicates. (**C**) Immunofluorescence analysis of 2iL and FA treated $RAS^{lox/lox}$ and $RAS^{KO}$ ESC stained for OTX2 (green), ERF (red) and NANOG (purple). DAPI was used to visualize nuclei. Scale bars, 100μm. (**D**) PCA plot of RNAseq datasets (three replicates) showing 2iL and FA treated $RAS^{lox/lox}$ and $RAS^{KO}$ ESC along with RNAseq datasets (two replicates) from a time course experiment during EpiLC induction (0, 1, 6, 12, 24, 36, 48 and 72 hours) (*20*). (**E**) PCA plot of RNAseq datasets showing 2iL and FA treated $RAS^{lox/lox}$ and $RAS^{KO}$ ESC along with RNAseq datasets from RSC (ESC lines grown in LIM (LIF, IWP2 (WNT inhibitor) and MEKi)), FSC, fPSC and XPSC (*7-10*). At least two replicates are shown. (**F**) Heatmap generated from RNAseq data from samples described in (E) showing the average from two or three replicates as applicable to each sample.

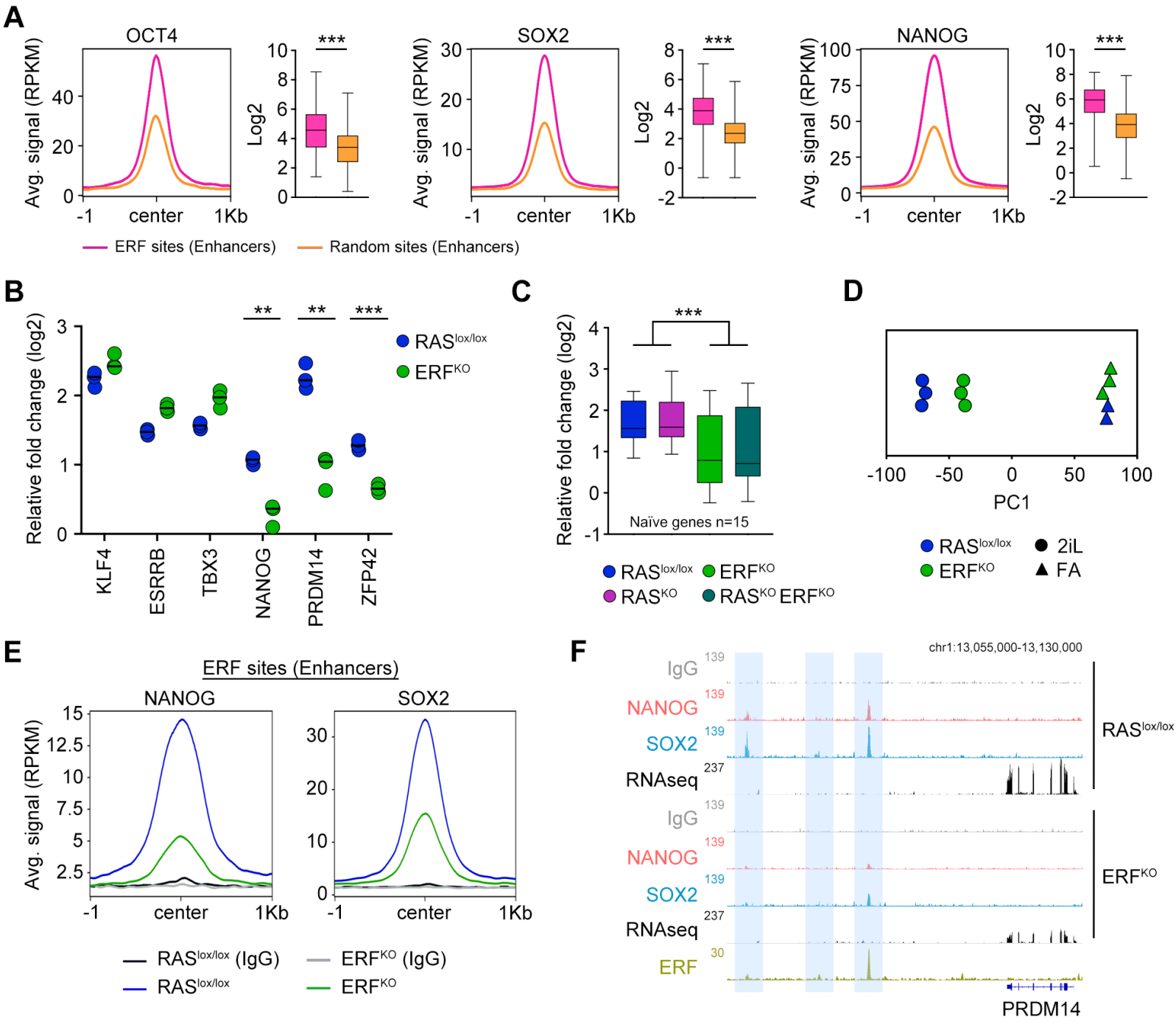
A
OCT4
SOX2
NANOG
Avg. signal (RPKM)
Log2
***
-1
center
1Kb
ERF sites (Enhancers)
Random sites (Enhancers)
B
Relative fold change (log2)
**
**
***
RASlox/lox
ERFKO
KLF4
ESRRB
TBX3
NANOG
PRDM14
ZFP42
C
Relative fold change (log2)
***
Naïve genes n=15
RASlox/lox
ERFKO
RASKO
RASKO ERFKO
D
PC1
RASlox/lox
ERFKO
2iL
FA
E
ERF sites (Enhancers)
NANOG
SOX2
Avg. signal (RPKM)
RASlox/lox (IgG)
RASlox/lox
ERFKO (IgG)
ERFKO
F
chr1:13,055,000-13,130,000
IgG
NANOG
SOX2
RNAseq
ERF
RASlox/lox
ERFKO
PRDM14

**Figure 4**

**Fig. 4. ERF ensures optimal naïve pluripotent transcription factor expression in ESC.** (**A**) ChIPseq read density plot (RPKM) showing OCT4, SOX2 and NANOG occupancy at 2074 ERF-binding sites at enhancers (pink) or 2074 randomly selected non-ERF bound enhancers (orange). Graphs show quantifications of the TF enrichment in each set of sites. *** = p<0.001, T-student. Data was obtained from (*47*). (**B**) Graph showing relative fold change (log2) expression of the indicated genes in $RAS^{lox/lox}$ and $ERF^{KO}$ ESC grown in 2iL. Genes showing at least a 50% reduction are highlighted. For each gene, data was normalized to the average across all samples. *** = p<0.001; ** = p<0.01. T-student. Data is shown as triplicates and was obtained from RNAseq datasets. (**C**) Graph showing the relative fold change (log2) expression of a subset of 15 naïve associated genes (*Klf4, Esrrb, Tfcp2l1, Tbx3, Klf2, Elf3, Klf8, Nanog, Prdm14, Tcl1, Zfp42, Nrob1, Prmd16, Dazl and Crxos*) in the different genotypes in 2iL conditions. For each gene, data was normalized to the average across all samples and was obtained from RNAseq datasets. *** = p<0.001. T-student. (**D**) Unidimensional PCA plot of RNAseq data of $RAS^{lox/lox}$ and $ERF^{KO}$ ESC cultured in naïve conditions (2iL) or induced to differentiate (FA) during 48 hours to EpiLC. Three replicates per condition are shown. PC1 separates samples by differentiation status. (**E**) Cut&Run read density plot (RPKM) showing NANOG and SOX2 occupancy in the set of 2074 ERF-binding sites at enhancers in $RAS^{lox/lox}$ (blue) and $ERF^{KO}$ (green) ESC cultured in 2iL. Corresponding inputs (IgG) are also shown as reference control. (**F**) Genome browser tracks showing NANOG and SOX2 occupancy and RNAseq RPKM read count at the PRDM14 gene in the indicated genotypes. ERF binding profile in $RAS^{KO}$ ESC is also shown. Inputs (IgG) are also shown as a reference control. ERF binding sites are highlighted.

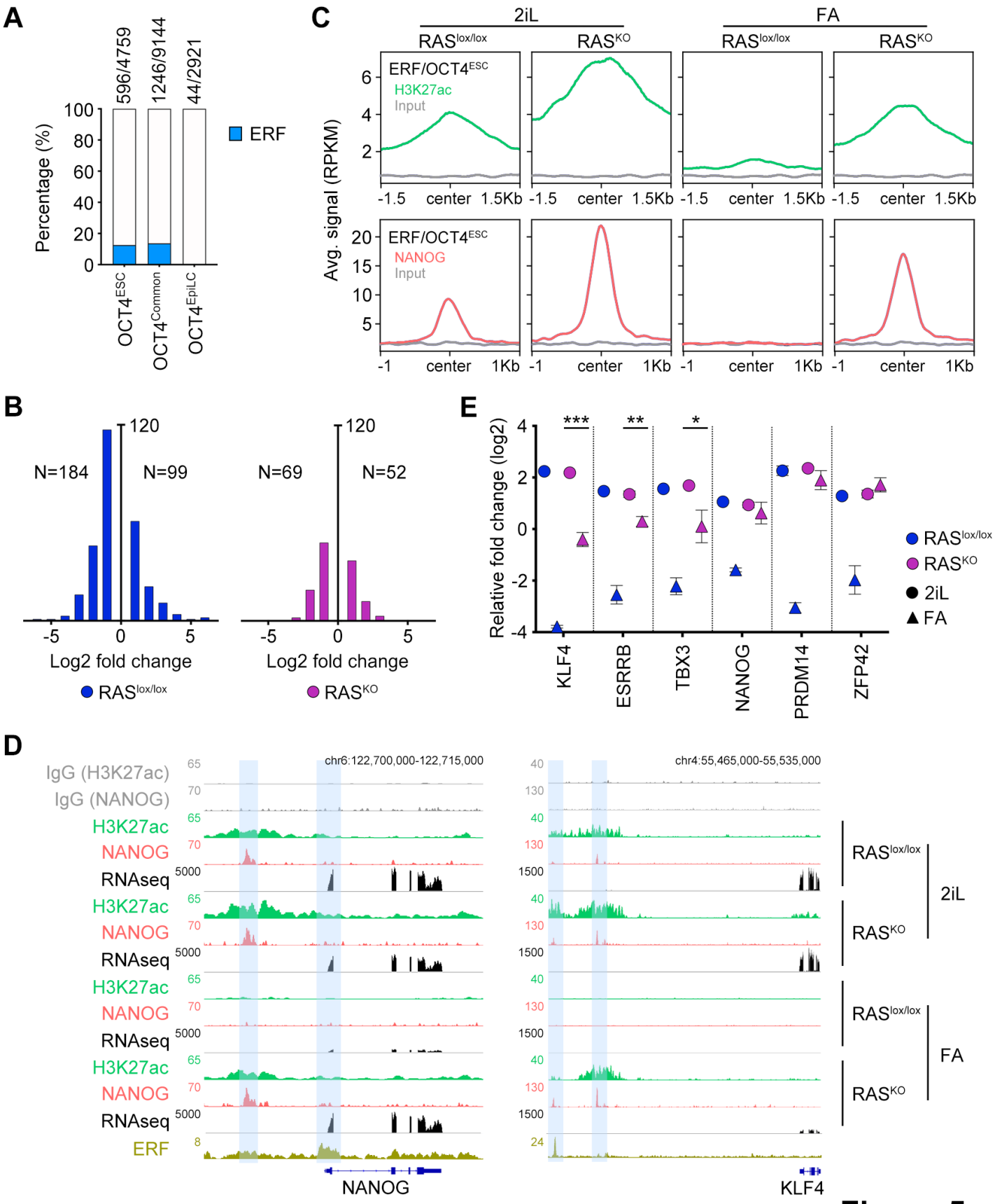
A
596/4759
1246/9144
44/2921
Percentage (%)
ERF
OCT4ESC
OCT4Common
OCT4EpiLC
B
N=184
N=99
N=69
N=52
Log2 fold change
RASlox/lox
RASKO
C
2iL
FA
ERF/OCT4ESC
H3K27ac
Input
NANOG
Avg. signal (RPKM)
-1.5 center 1.5Kb
-1 center 1Kb
D
IgG (H3K27ac)
IgG (NANOG)
RNAseq
ERF
chr6:122,700,000-122,715,000
chr4:55,465,000-55,535,000
NANOG
KLF4
E
Relative fold change (log2)
KLF4
ESRRB
TBX3
NANOG
PRDM14
ZFP42
2iL
FA

**Figure 5**

**Fig. 5. The naïve pluripotent transcription factor network is active in FA-RAS$^{KO}$ ESC.** (**A**) Plot showing the percentage of OCT4 binding sites co-occupied by ERF in ESC, EpiLC and common between ESC and EpiLC. (**B**) Histogram plots showing fold expression changes (log2) for genes associated to ERF/OCT4$^{ESC}$ that are characterized by differential expression between ESC and EpiLC in RAS$^{lox/lox}$ and RAS$^{KO}$ cells. N indicates the total number of genes that are up or downregulated. Genes were associated at every binding site by proximity using GREAT (ref PMID: 20436461). Data was obtained from RNAseq datasets. (**C**) Cut&Run read density plot (RPKM) showing H3K27ac (plots above, green) and NANOG (plots below, red) occupancy in ERF/OCT4$^{ESC}$ sites in RAS$^{lox/lox}$ and RAS$^{KO}$ cultured in 2iL or differentiated to EpiLC (FA). Corresponding inputs (IgG) are also shown as reference control. (**D**) Genome browser tracks showing H3K27ac deposition, NANOG, ERF occupancy and RNAseq RPKM read count at the KLF4 and NANOG genes in the indicated genotypes. Inputs (IgG) are also shown as a reference control. (**E**) Graph showing the relative fold change (log2) expression of the indicated ERF-bound super-enhancer associated genes in RAS$^{lox/lox}$ and RAS$^{KO}$ cultured in 2iL or differentiated to EpiLC (FA). Genes showing at least a 50% reduction are highlighted. For each gene, data was normalized to the average across all samples. *** = $p<0.001$; ** = $p<0.01$; *=<0.05 T-student. Data shown are averages from triplicates and was obtained from RNAseq datasets.

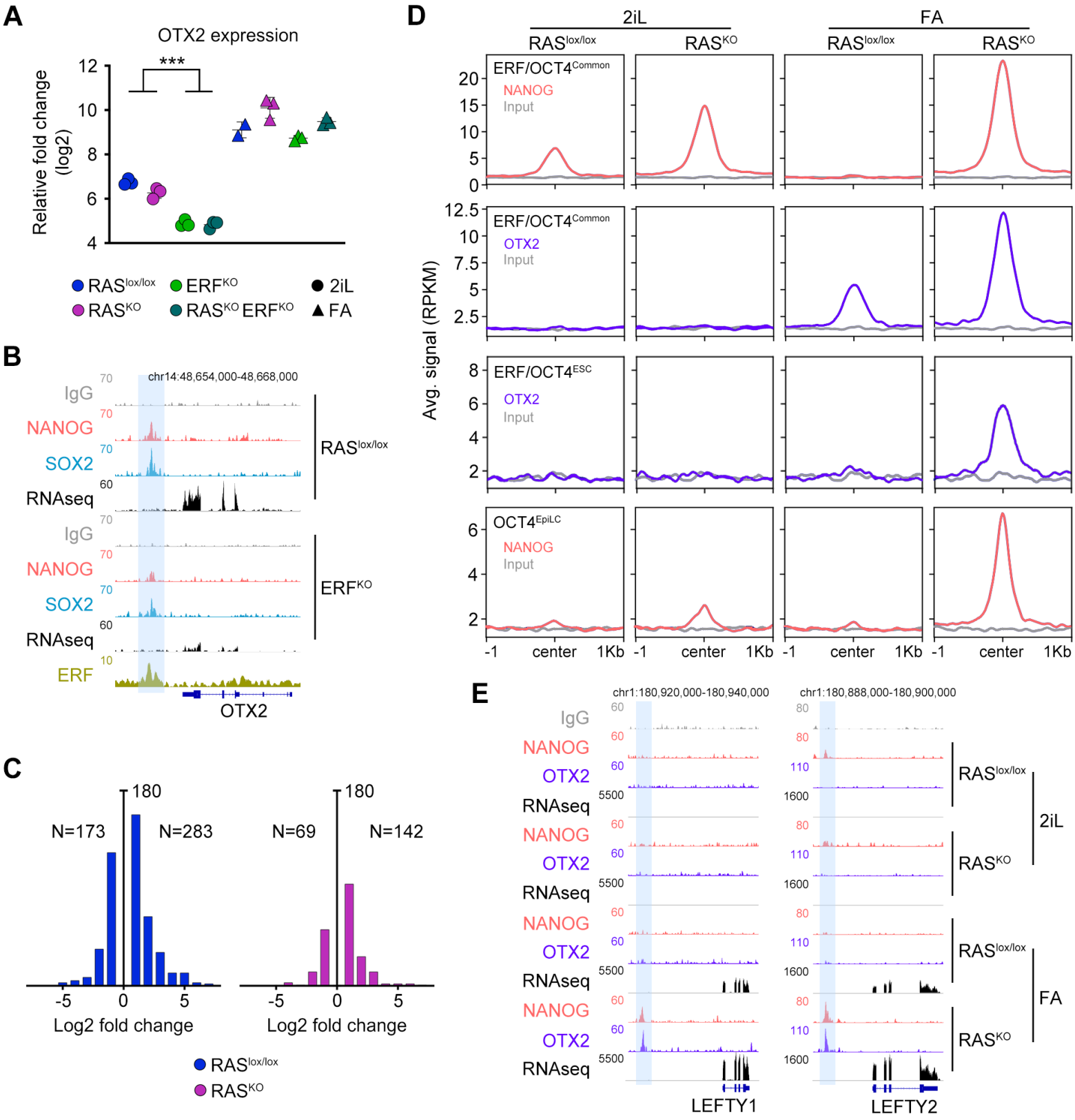
A
OTX2 expression
***
Relative fold change (log2)
RASlox/lox
RASKO
ERFKO
RASKO ERFKO
2iL
FA
B
chr14:48,654,000-48,668,000
IgG
NANOG
SOX2
RNAseq
ERF
RASlox/lox
ERFKO
OTX2
C
N=173
N=283
N=69
N=142
Log2 fold change
Log2 fold change
RASlox/lox
RASKO
D
2iL
FA
RASlox/lox
RASKO
ERF/OCT4Common
NANOG
Input
ERF/OCT4Common
OTX2
Input
ERF/OCT4ESC
OTX2
Input
OCT4EpiLC
NANOG
Input
Avg. signal (RPKM)
-1
center
1Kb
E
chr1:180,920,000-180,940,000
chr1:180,888,000-180,900,000
IgG
NANOG
OTX2
RNAseq
RASlox/lox
RASKO
2iL
FA
LEFTY1
LEFTY2

**Figure 6**

**Fig. 6. OTX2 shows promiscuous binding in naïve and primed genes in FA-RAS$^{KO}$ ESC.** (**A**) Plot showing the relative fold change (log2) expression for OTX2 in ESC from all genotypes cultured in 2iL or differentiated to EpiLC (FA). Data was normalized to the average across all samples. ***= p<0.001; T-student. Data shown from triplicates and was obtained from RNAseq datasets. (**B**) Genome browser tracks showing SOX2 and NANOG occupancy and RNAseq RPKM read count at the OTX2 gene in RAS$^{lox/lox}$ and ERF$^{KO}$ ESC cultured in 2iL. ERF binding profile in RAS$^{KO}$ ESC is also shown. Inputs (IgG) are also shown as a reference control. ERF binding sites are highlighted. (**C**) Histogram plots showing fold expression changes (log2) for genes associated to ERF/OCT4$^{Common}$ that showed differential expression between ESC and EpiLC in RAS$^{lox/lox}$ and RAS$^{KO}$ cells. N indicates the total number of genes that are up or downregulated. Genes were associated at every binding site by proximity using GREAT (ref PMID: 20436461). Data was obtained from RNAseq datasets. (**D**) Cut&Run read density plot (RPKM) showing NANOG (red) and OTX2 (purple) occupancy in the indicated ERF/OCT4$^{Common}$, ERF/OCT4$^{ESC}$ and ERF/OCT4$^{EpiLC}$ sites in RAS$^{lox/lox}$ and RAS$^{KO}$ ESC cultured in 2iL or differentiated to EpiLC (FA). Corresponding inputs (IgG) are also shown as reference control. (**E**) Genome browser tracks showing NANOG and OTX2 occupancy and RNAseq RPKM read count at the LEFTY1 and LEFTY2 genes in RAS$^{lox/lox}$ and RAS$^{KO}$ ESC cultured in 2iL or differentiated to EpiLC (FA). Inputs (IgG) are also shown as a reference control. Blue squares showed ERF binding sites.

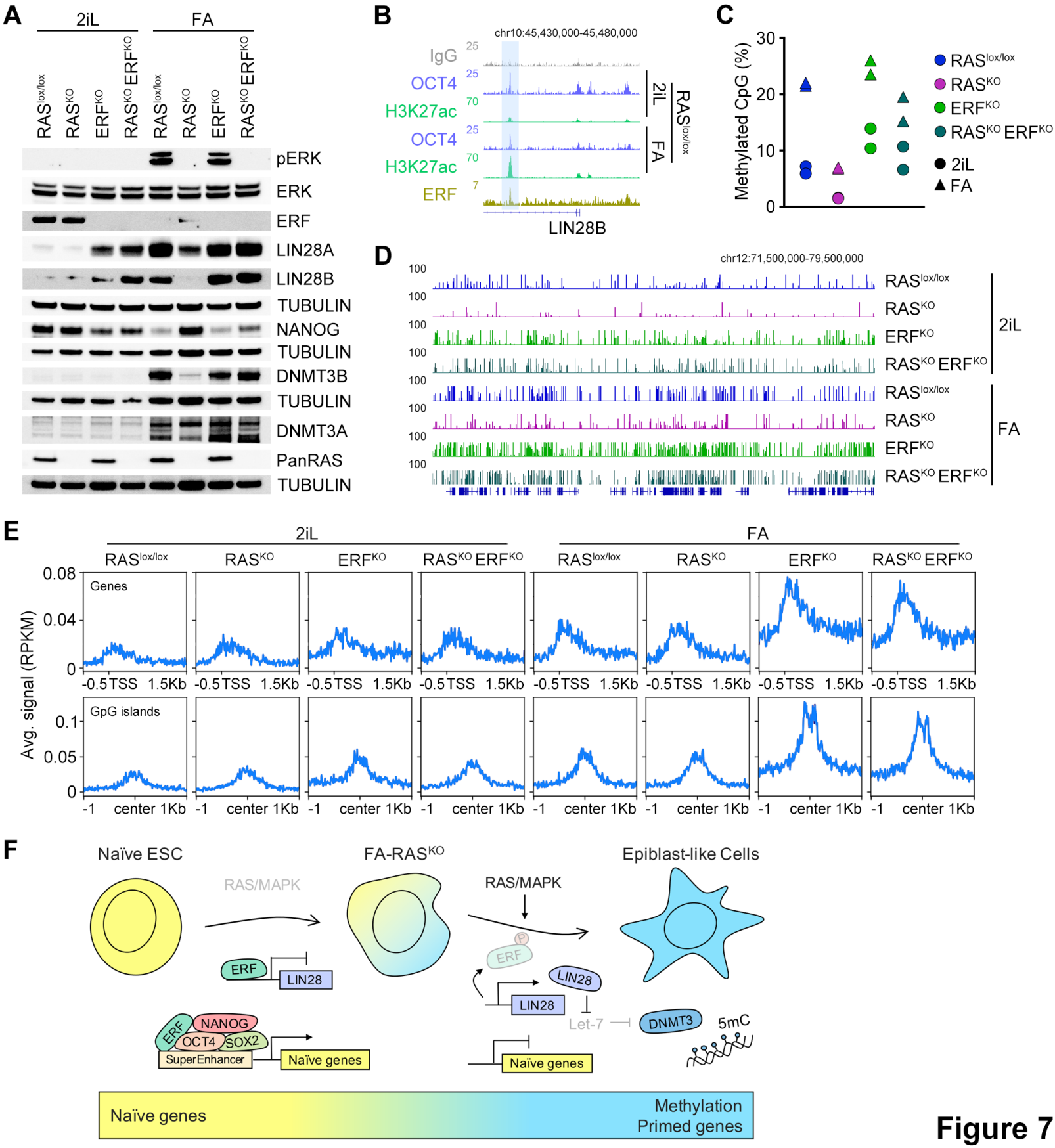
A
2iL
FA
RASlox/lox
RASKO
ERFKO
RASKO ERFKO
pERK
ERK
ERF
LIN28A
LIN28B
TUBULIN
NANOG
TUBULIN
DNMT3B
TUBULIN
DNMT3A
PanRAS
TUBULIN
B
chr10:45,430,000-45,480,000
IgG
OCT4
H3K27ac
OCT4
H3K27ac
ERF
2iL
FA
RASlox/lox
LIN28B
C
Methylated CpG (%)
RASlox/lox
RASKO
ERFKO
RASKO ERFKO
2iL
FA
D
chr12:71,500,000-79,500,000
RASlox/lox
RASKO
ERFKO
RASKO ERFKO
2iL
FA
E
2iL
FA
Genes
GpG islands
Avg. signal (RPKM)
-0.5TSS 1.5Kb
-1 center 1Kb
F
Naïve ESC
RAS/MAPK
ERF
LIN28
NANOG
OCT4
SOX2
SuperEnhancer
Naïve genes
FA-RASKO
RAS/MAPK
ERF
LIN28
LIN28
Let-7
DNMT3
5mC
Naïve genes
Epiblast-like Cells
Naïve genes
Methylation
Primed genes

**Figure 7**

**Fig. 7. ERF controls the levels of *de novo* methylation during transition to EpiLC.** (**A**) Western blot analysis of the indicated proteins performed in ESC from all genotypes cultured in 2iL or differentiated to EpiLC (FA). Tubulin levels for the corresponding blots are shown as a loading control. One representative experiment is shown but at least two independent clones per condition and genotype were used. (**B**) Genome browser tracks showing H3K27ac deposition and OCT4 occupancy at the LIN28B gene in $RAS^{lox/lox}$ ESC cultured in 2iL or differentiated to EpiLC (FA). ERF binding profile in $RAS^{KO}$ ESC is also shown. Inputs (IgG) are also shown as a reference control. ERF binding sites are highlighted. (**C**) Graph showing the percentage of methylated CpG sites identified by RRBS in ESC from all genotypes cultured in 2iL or differentiated to EpiLC (FA). (**D**) Genome browser tracks showing as a representative example the level of methylation at CpG sites in a region of chromosome 12 in ESC from all genotypes cultured in 2iL or differentiated to EpiLC (FA). (**E**) %CpG methylation averaged across the TSS of all protein-coding mouse genes (upper panels) or centered at CpG islands (lower panels) in ESC from all genotypes cultured in 2iL or differentiated to EpiLC (FA). (**F**) Schematic model showing the dual role of ERF during the naïve to primed pluripotent transition. In the absence of FGF signaling, ERF ensures an optimal level of expression for naïve transcription factors. Following ERF phosphorylation and gene silencing, ESC are able to exit and transition into EpiLC along with global CpG methylation and silencing of the naïve transcriptional network.

# Supplementary materials for

## The ETS Transcription Factor ERF controls the exit from the naïve pluripotent state in a MAPK-dependent manner

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**The PDF file includes:**

Figs. S1 to S10
Tables S1 to S3

**Other Supplementary Materials for this manuscript include the following:**

Supplementary Data S1 to S9

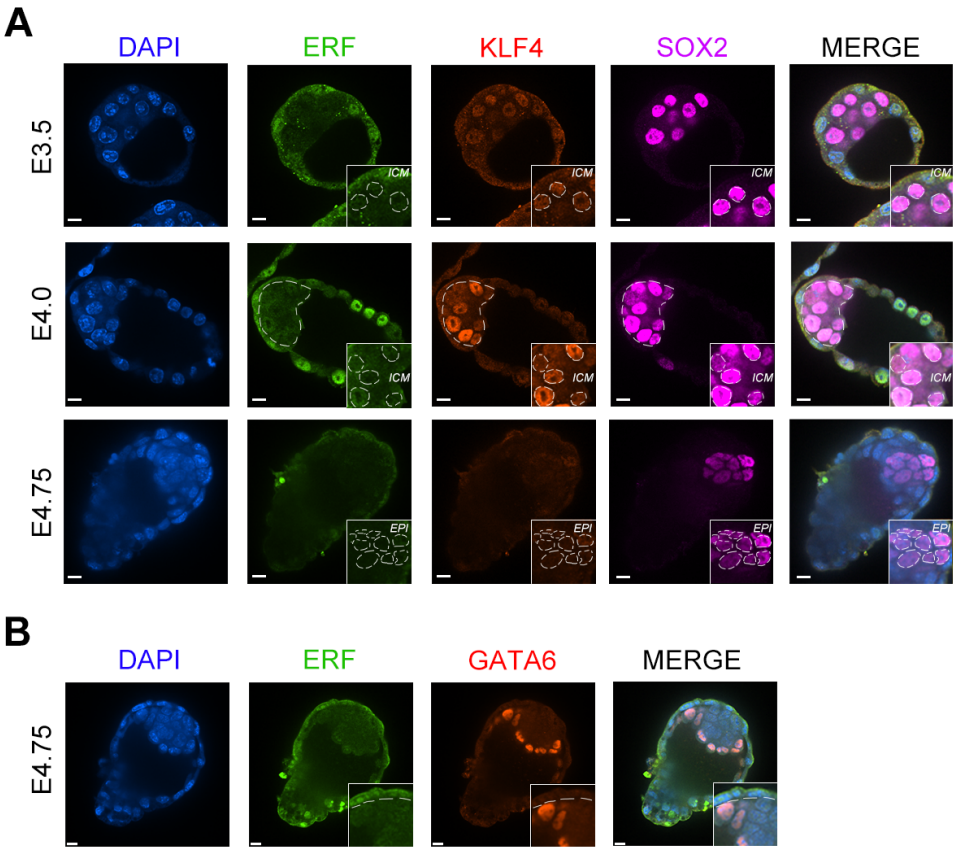
A
DAPI
ERF
KLF4
SOX2
MERGE
E3.5
E4.0
E4.75
ICM
EPI
B
DAPI
ERF
GATA6
MERGE
E4.75

**Figure S1**

**Figure S1: ERF expression decreases upon exit from naïve pluripotency.** (**A**) Immunofluorescence analysis of KLF4, SOX2 and ERF in mouse embryos at E3.5, E4.0 and E4.75. Note that ERF is expressed in both ICM and TE. However, ERF and KLF4 are mostly downregulated in epiblast cells while SOX2 is still expressed in embryos at E4.75. Dashed line highlights the ICM/EPI. DAPI was used to visualize nuclei. Scale bars, 10μm. (**B**) Immunofluorescence analysis of GATA6 and ERF in mouse embryos at E4.75. Note that ERF is mostly downregulated in the specified PrE. DAPI was used to visualize nuclei. Scale bars, 10μm.

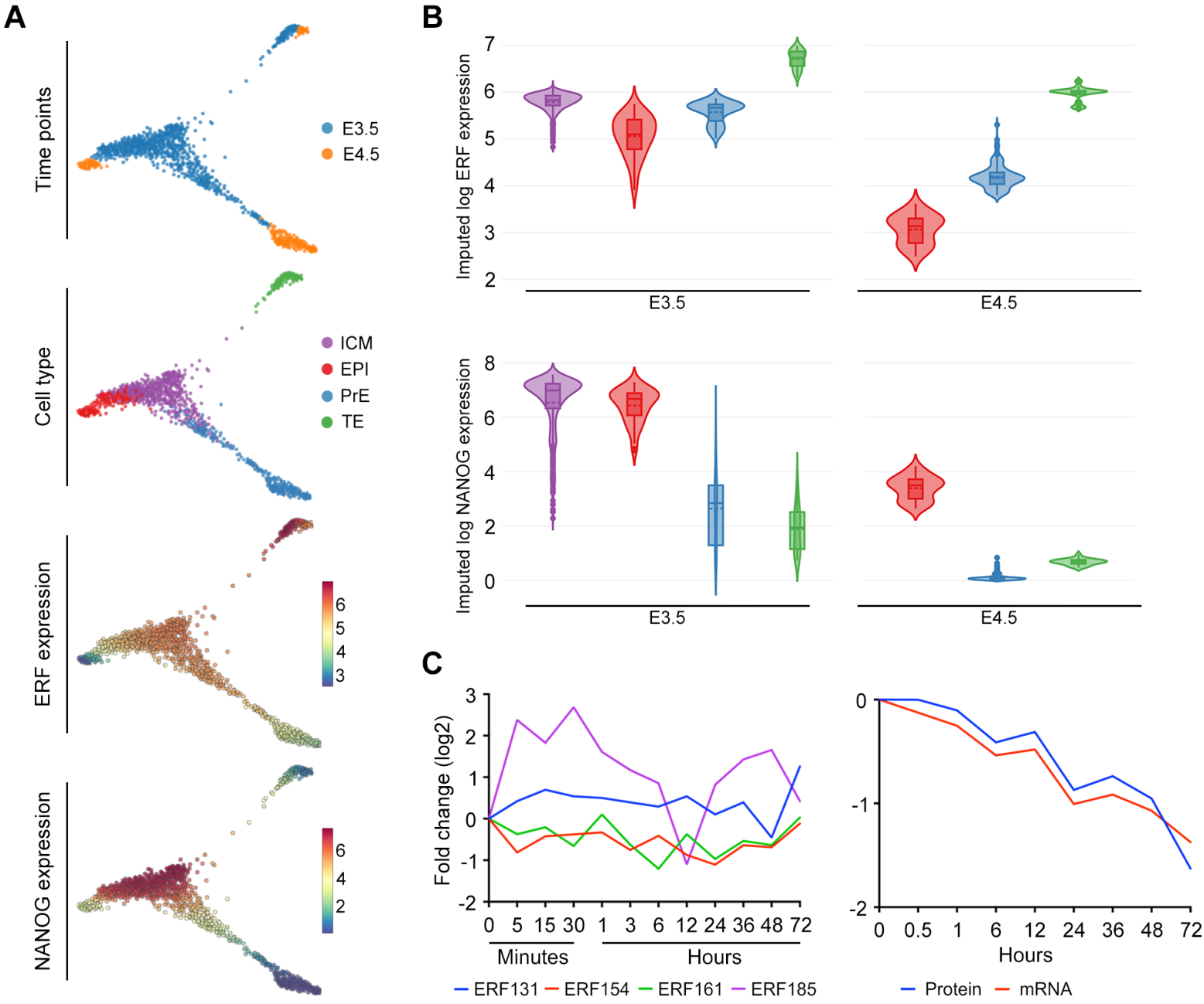
A
Time points
E3.5
E4.5
Cell type
ICM
EPI
PrE
TE
ERF expression
6
5
4
3
NANOG expression
6
4
2
B
Imputed log ERF expression
7
6
5
4
3
2
E3.5
E4.5
Imputed log NANOG expression
8
6
4
2
0
E3.5
E4.5
C
Fold change (log2)
3
2
1
0
-1
-2
0 5 15 30 1 3 6 12 24 36 48 72
Minutes
Hours
ERF131 ERF154 ERF161 ERF185
0
-1
-2
0 0.5 1 6 12 24 36 48 72
Hours
Protein mRNA

**Figure S2**

**Figure S2: Exit from naïve pluripotency correlates with decreased levels of ERF.** (**A**) Forced-directed layouts of E3.5 and E4.5 single cell RNAseq data showing the temporal expression for ERF and NANOG in the ICM (inner cell mass, purple), EPI (epiblast, red), PrE (primitive endoderm, light blue) and TE (throphectoderm, light green). Cells are colored by timepoint or cell type. Data was obtained from (*16*). Cells are colored by gene expression post-imputation with the MAGIC algorithm (*16, 67*). (**B**) Violin plots showing imputed log expression for ERF (upper panel) and NANOG (lower panel) in ICM, EPI, PrE and TE at E3.5 and E4.5. For (A) and (B), plots were obtained from https://endoderm-explorer.com/. (**C**) Temporal dynamics of relative ERF phosphorylation levels (left panel) and ERF protein and mRNA levels (right panel) compared to timepoint 0 hours during the transition from ESC to EpiLC. Data was obtained from (20).

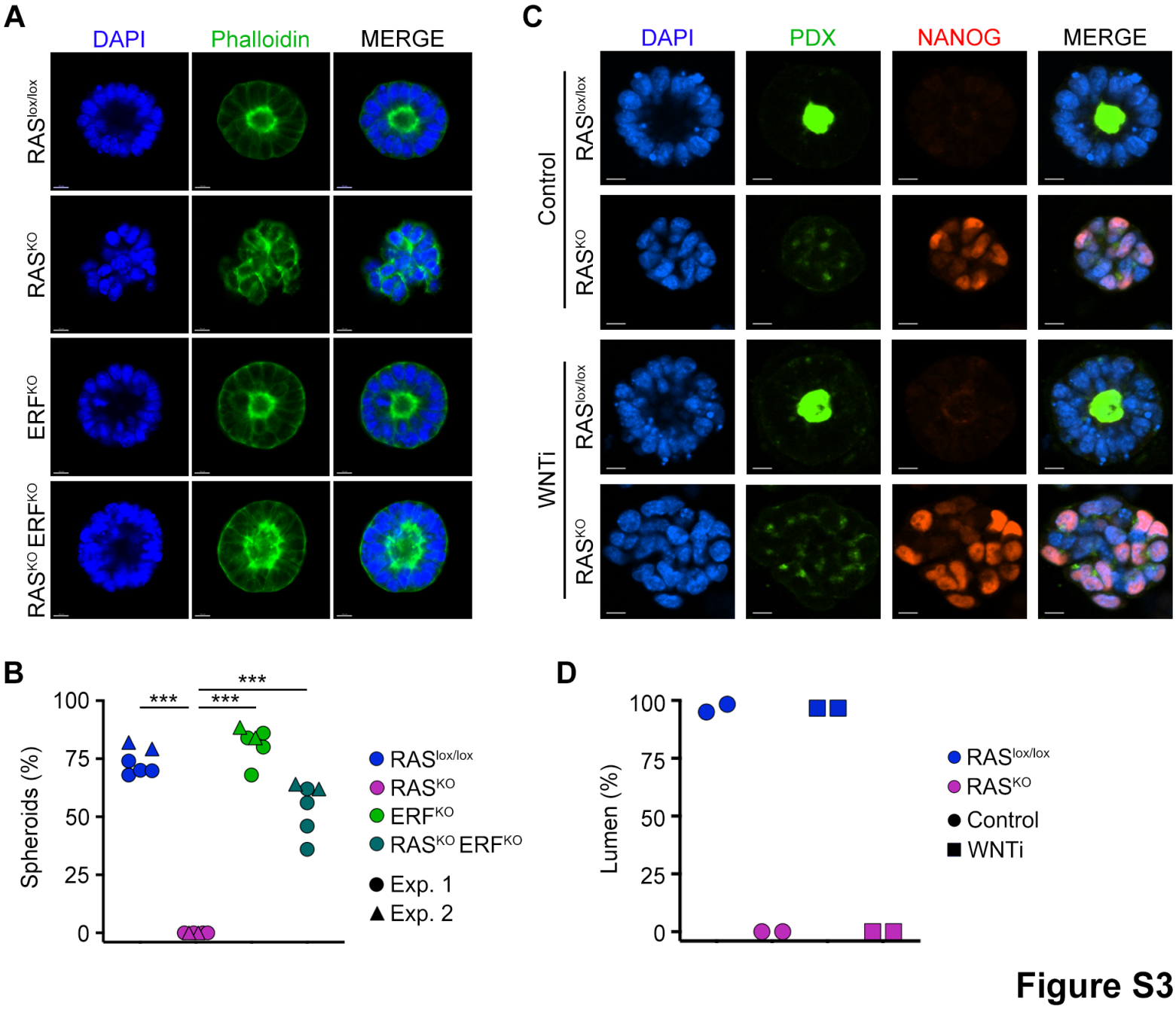
A
DAPI
Phalloidin
MERGE
RASlox/lox
RASKO
ERFKO
RASKO ERFKO
C
DAPI
PDX
NANOG
MERGE
Control
WNTi
RASlox/lox
RASKO
B
Spheroids (%)
100
75
50
25
0
***
***
***
RASlox/lox
RASKO
ERFKO
RASKO ERFKO
Exp. 1
Exp. 2
D
Lumen (%)
100
75
50
25
0
RASlox/lox
RASKO
Control
WNTi

**Figure S3**

**Figure S3: Downregulation of ERF is necessary for successful exit from naïve pluripotency**. (**A**) Central confocal optical sections of $RAS^{lox/lox}$, $ERF^{KO}$, $RAS^{KO}$, and $RAS^{KO}$; $ERF^{KO}$ embryonic cell rosettes embedded in matrigel 48 hours after seeding and stained with phalloidin (green). DAPI was used to visualize nuclei. Scale bars, 10μm. (**B**) Graph showing the percentage of morphologically organized embryonic rosettes in all genotypes based on the staining from (A). Two independent experiments are shown and at least, a total of 50 rosettes were counted. ***=$p<0.001$. (**C**) Central confocal optical sections of $RAS^{lox/lox}$ and $RAS^{KO}$ embryonic cell rosettes embedded in matrigel 48 hours after seeding cultured with or without 2μM IWR-1 and stained with NANOG (red) and PDX (green). DAPI was used to visualize nuclei. Scale bars, 10μm. (**D**) Graph showing the percentage of embryonic rosettes containing lumen based on the staining from (C). Two independent experiments are shown and at least, a total of 60 rosettes was counted.

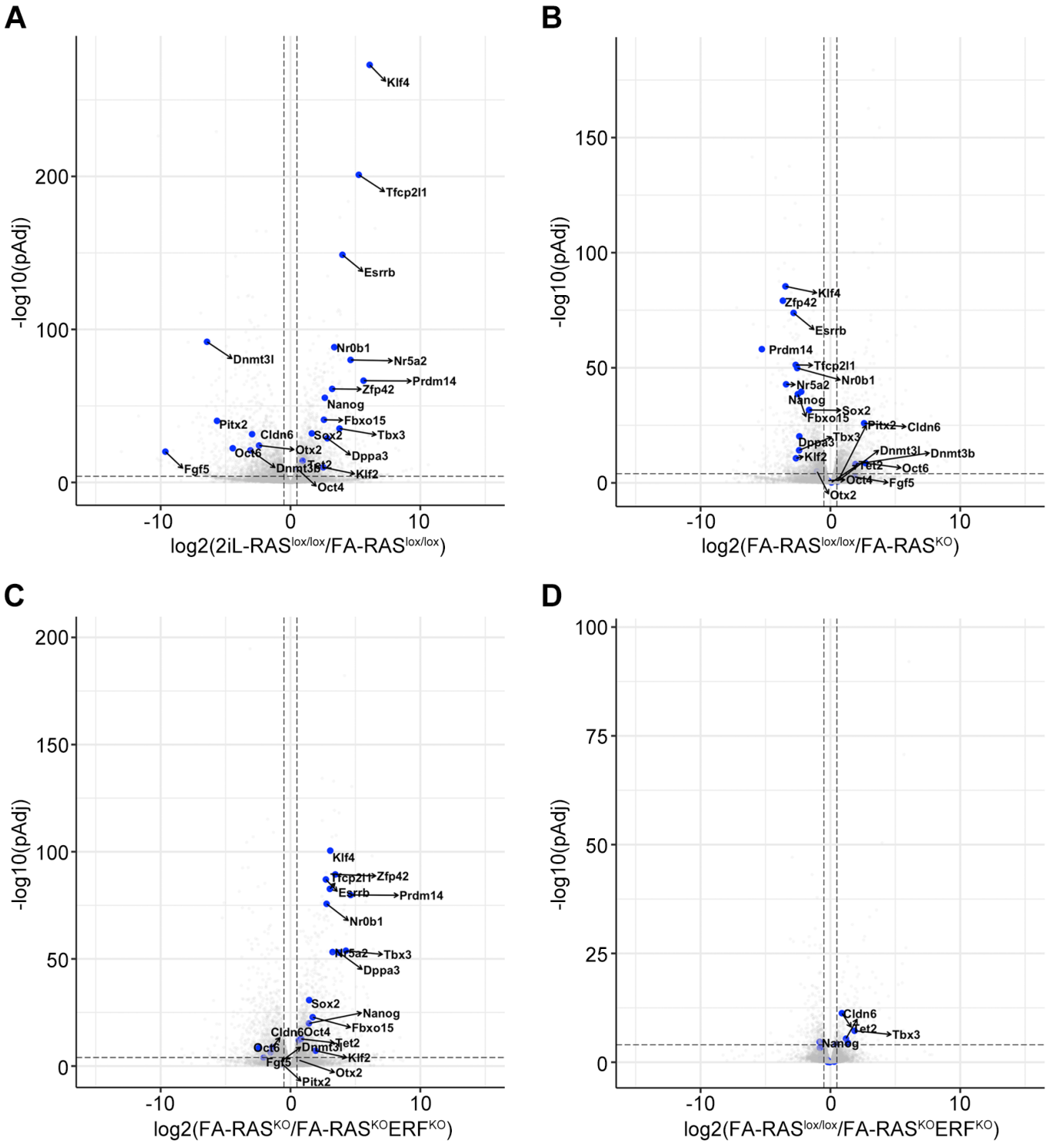
A
-log10(pAdj)
log2(2iL-RAS^lox/lox/FA-RAS^lox/lox)
Klf4
Tfcp2l1
Esrrb
Nr0b1
Nr5a2
Prdm14
Zfp42
Nanog
Fbxo15
Sox2
Tbx3
Dppa3
Tet2
Klf2
Oct4
Otx2
Dnmt3l
Pitx2
Cldn6
Oct6
Fgf5
B
-log10(pAdj)
log2(FA-RAS^lox/lox/FA-RAS^KO)
Klf4
Zfp42
Esrrb
Prdm14
Tfcp2l1
Nr0b1
Nr5a2
Nanog
Sox2
Fbxo15
Pitx2
Cldn6
Tbx3
Dppa3
Klf2
Dnmt3l
Dnmt3b
Tet2
Oct6
Oct4
Fgf5
Otx2
C
-log10(pAdj)
log2(FA-RAS^KO/FA-RAS^KOERF^KO)
Klf4
Tfcp2l1
Zfp42
Esrrb
Prdm14
Nr0b1
Nr5a2
Tbx3
Dppa3
Sox2
Nanog
Fbxo15
Cldn6
Oct4
Tet2
Oct6
Dnmt3l
Klf2
Fgf5
Otx2
Pitx2
D
-log10(pAdj)
log2(FA-RAS^lox/lox/FA-RAS^KOERF^KO)
Cldn6
Tet2
Tbx3
Nanog

**Figure S4**

**Figure S4: Gene expression changes in ESC cultured under naïve (2iL) or differentiated (FA) conditions.** (**A-D**) Volcano plots showing differentially expressed genes in relevant sample comparisons. The set of 22 naïve and primed-associated genes used to generate the heatmaps from Fig. 3B and F are highlighted. Note how the intermediate transcriptional state observed in FA-RAS$^{KO}$ ESC is mostly rescued in FA-RAS$^{KO}$ERF$^{KO}$ ESC.

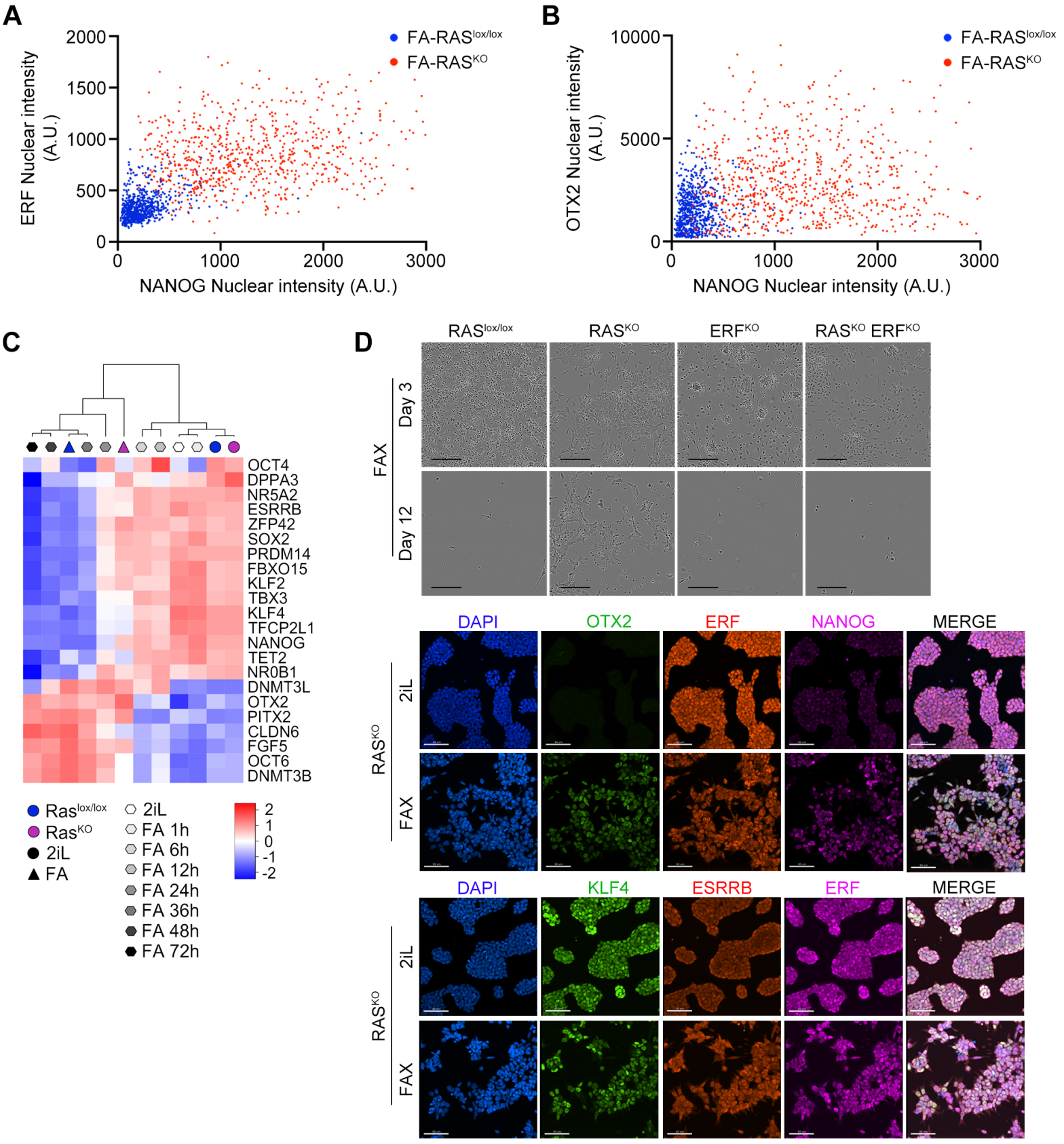
A
ERF Nuclear intensity (A.U.)
NANOG Nuclear intensity (A.U.)
FA-RASlox/lox
FA-RASKO
B
OTX2 Nuclear intensity (A.U.)
NANOG Nuclear intensity (A.U.)
C
OCT4
DPPA3
NR5A2
ESRRB
ZFP42
SOX2
PRDM14
FBXO15
KLF2
TBX3
KLF4
TFCP2L1
NANOG
TET2
NR0B1
DNMT3L
OTX2
PITX2
CLDN6
FGF5
OCT6
DNMT3B
Raslox/lox
RasKO
2iL
FA
2iL
FA 1h
FA 6h
FA 12h
FA 24h
FA 36h
FA 48h
FA 72h
D
RASlox/lox
RASKO
ERFKO
RASKO ERFKO
FAX
Day 3
Day 12
DAPI
OTX2
ERF
NANOG
MERGE
RASKO
2iL
FAX
DAPI
KLF4
ESRRB
ERF
MERGE

**Figure S5**

**Figure S5: ERF controls the transition to primed pluripotency.** (**A, B**) Graph plots showing quantified mean intensity levels of NANOG/ERF (**A**) and OTX2/NANOG (**B**) in FA-RAS$^{lox/lox}$ and FA-RAS$^{KO}$ ESC. ERF as well as NANOG are mostly downregulated in FA-RAS$^{lox/lox}$ whereas they express OTX2. Note the heterogeneity in the expression of these markers in FA-RAS$^{KO}$ ESC. Number of cells plotted: 750. (**C**) Heatmap generated from RNAseq datasets showing 2iL and FA treated RAS$^{lox/lox}$ and RAS$^{KO}$ ESC along with RNAseq datasets from a time course experiment during EpiLC induction (0, 1, 6, 12, 24, 36, 48 and 72 hours) (*20*). Shown are the averaged values of at least 2 replicates. (**D**) Bright field images of RAS$^{lox/lox}$, ERF$^{KO}$, RAS$^{KO}$, and RAS$^{KO}$; ERF$^{KO}$ ESC cultures in EpiLC media (FAX) 3 and 12 days after the media switch (upper panels). Note that only EpiLC cultures were able to be maintained with RAS$^{KO}$ ESC. Scale bars, 200μm. In the lower panel, immunofluorescence analysis of 2iL and FAX treated RAS$^{KO}$ ESC and stained for OTX2 (green), ERF (red) and NANOG (purple) are shown. DAPI was used to visualize nuclei. Scale bars, 80μm.

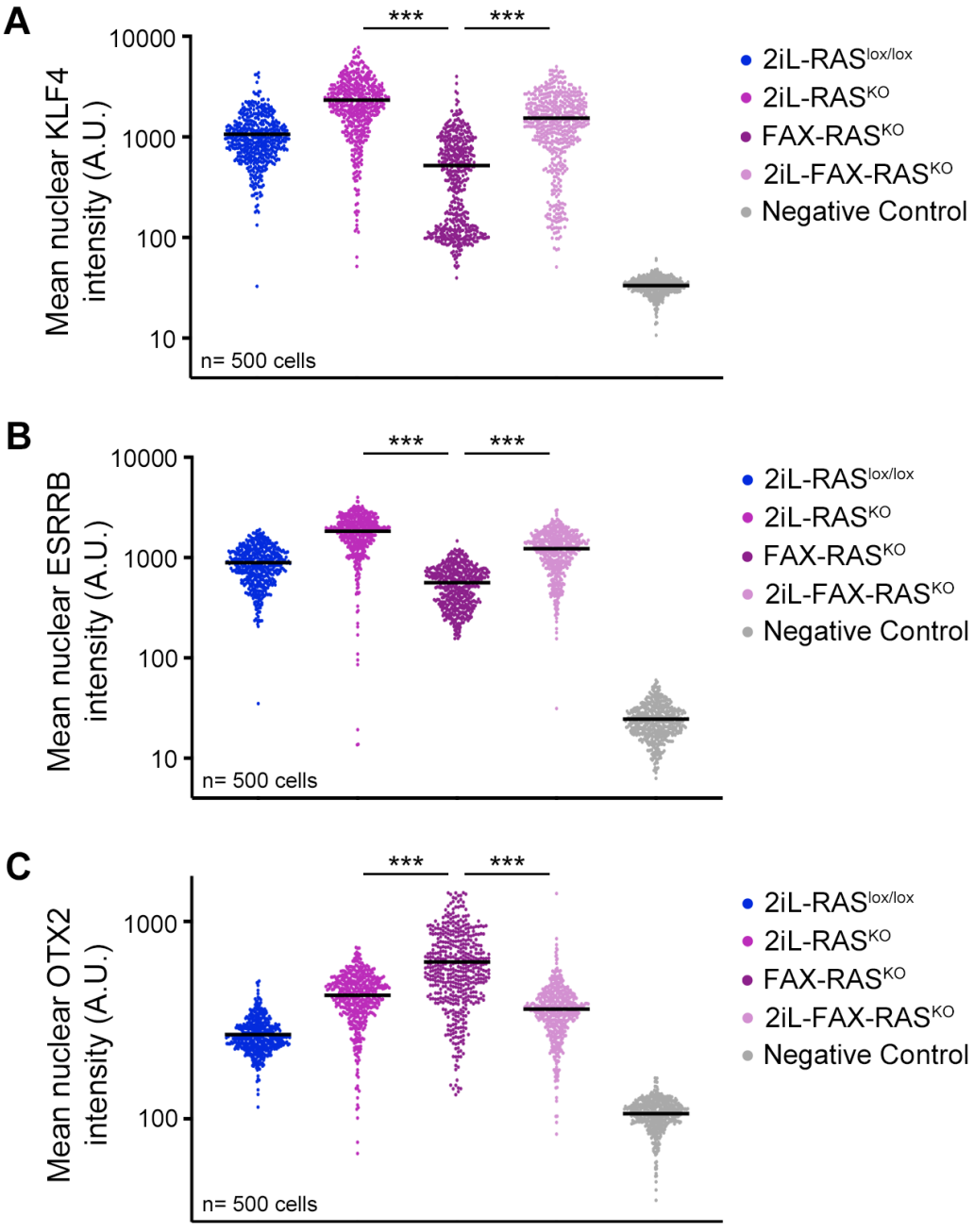
A
Mean nuclear KLF4 intensity (A.U.)
10000
1000
100
10
***
***
n= 500 cells
2iL-RASlox/lox
2iL-RASKO
FAX-RASKO
2iL-FAX-RASKO
Negative Control
B
Mean nuclear ESRRB intensity (A.U.)
10000
1000
100
10
***
***
n= 500 cells
2iL-RASlox/lox
2iL-RASKO
FAX-RASKO
2iL-FAX-RASKO
Negative Control
C
Mean nuclear OTX2 intensity (A.U.)
1000
100
***
***
n= 500 cells
2iL-RASlox/lox
2iL-RASKO
FAX-RASKO
2iL-FAX-RASKO
Negative Control

**Figure S6**

**Figure S6: The intermediate pluripotent state in FA-RAS$^{KO}$ ESC is reversible.** (**A-C**) High-throughput imaging (HTI) quantification of the mean nuclear intensity for KLF4 (**A**), ESRRB (**B**) and OTX2 (**C**) in 2iL-RAS$^{lox/lox}$, 2i-RAS$^{KO}$, FAX-RAS$^{KO}$ and 2iL-FAX-RAS$^{KO}$ (FAX-growing ESC transferred to 2iL conditions) ESC. Data are representative of at least two independent clones. Note how the expression of these markers in FAX-RAS$^{KO}$ transferred to 2iL conditions is restored to a similar level compared to 2iL-RAS$^{KO}$. Center lines indicate mean values. *** = $p<0.001$. T-student. Negative control indicates no primary antibody. Number of cells: 500.

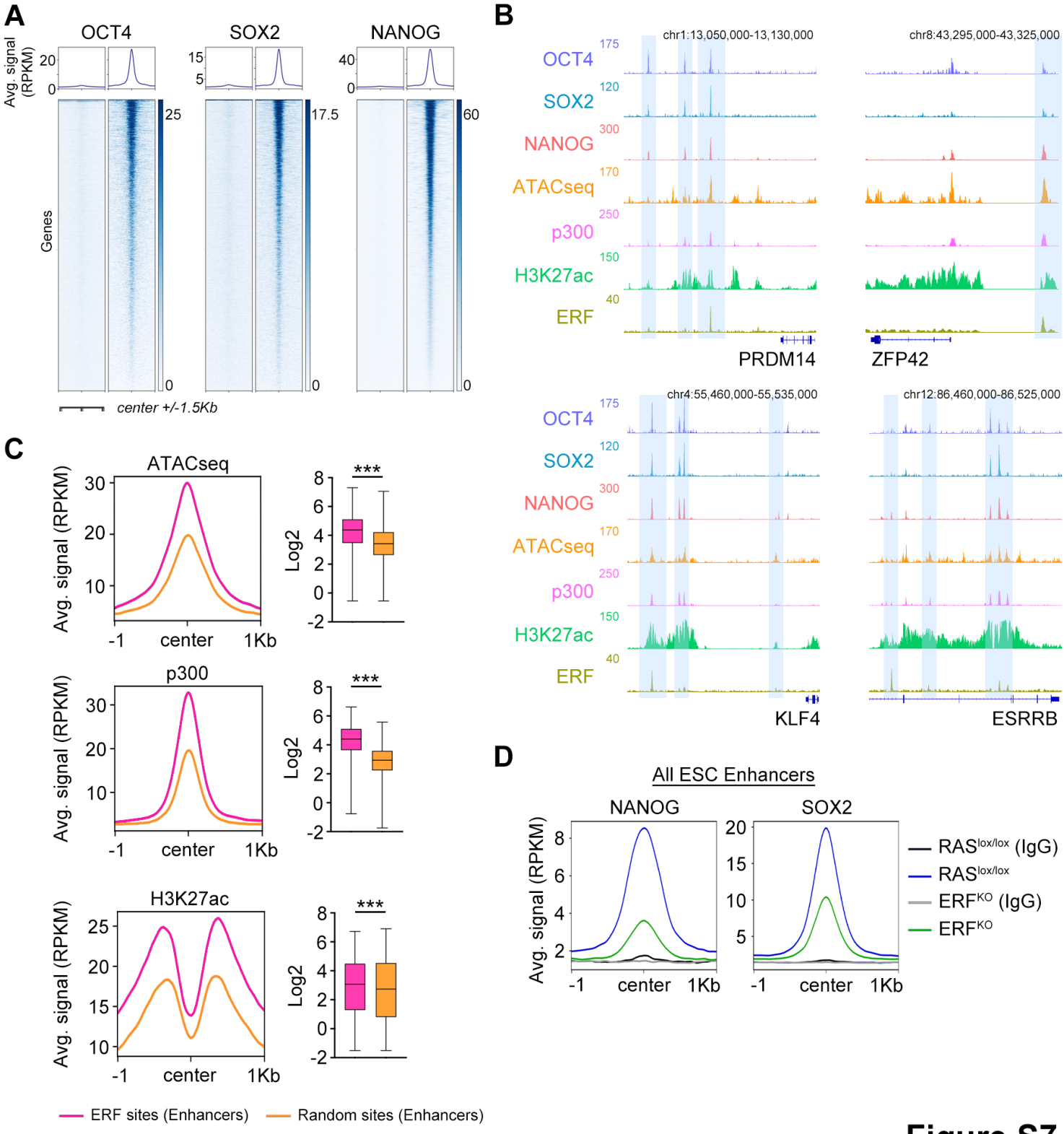
A
OCT4
SOX2
NANOG
Avg. signal (RPKM)
Genes
center +/-1.5Kb
B
chr1:13,050,000-13,130,000
chr8:43,295,000-43,325,000
OCT4
SOX2
NANOG
ATACseq
p300
H3K27ac
ERF
PRDM14
ZFP42
chr4:55,460,000-55,535,000
chr12:86,460,000-86,525,000
KLF4
ESRRB
C
ATACseq
p300
H3K27ac
Avg. signal (RPKM)
Log2
center
1Kb
ERF sites (Enhancers)
Random sites (Enhancers)
D
All ESC Enhancers
NANOG
SOX2
RASlox/lox (IgG)
RASlox/lox
ERFKO (IgG)
ERFKO

**Figure S7**

**Figure S7: Chromatin-bound ERF ensures an optimal naïve pluripotency state.** (**A**) Heatmaps showing OCT4, SOX2 and NANOG (47) occupancy at the set of 5529 ERF-bound sites. (**B**) Genome browser tracks showing OCT4, SOX2, NANOG (*47*), H3K27ac, P300 (*27*), ATACseq (*68*) and ERF (11) normalized read count at PRDM14, ESRRB, KLF4 and REX1 (ZFP42) naïve associated genes in ESC. ERF binding sites are highlighted. (**C**) ChIPseq read density plot showing H3K27ac, p300 (*27*), as well as ATACseq signal (*68*) at 2074 ERF-binding sites at enhancers (pink) or 2074 randomly selected non-ERF bound enhancers (orange). *** = $p<0.001$, T-student. (**D**) Cut&Run read density plot showing SOX2 and NANOG occupancy in all ESC enhancers (10672) in $RAS^{lox/lox}$ (blue) and $ERF^{KO}$ (green) ESC cultured in 2iL. Corresponding inputs (IgG) are also shown as reference control.

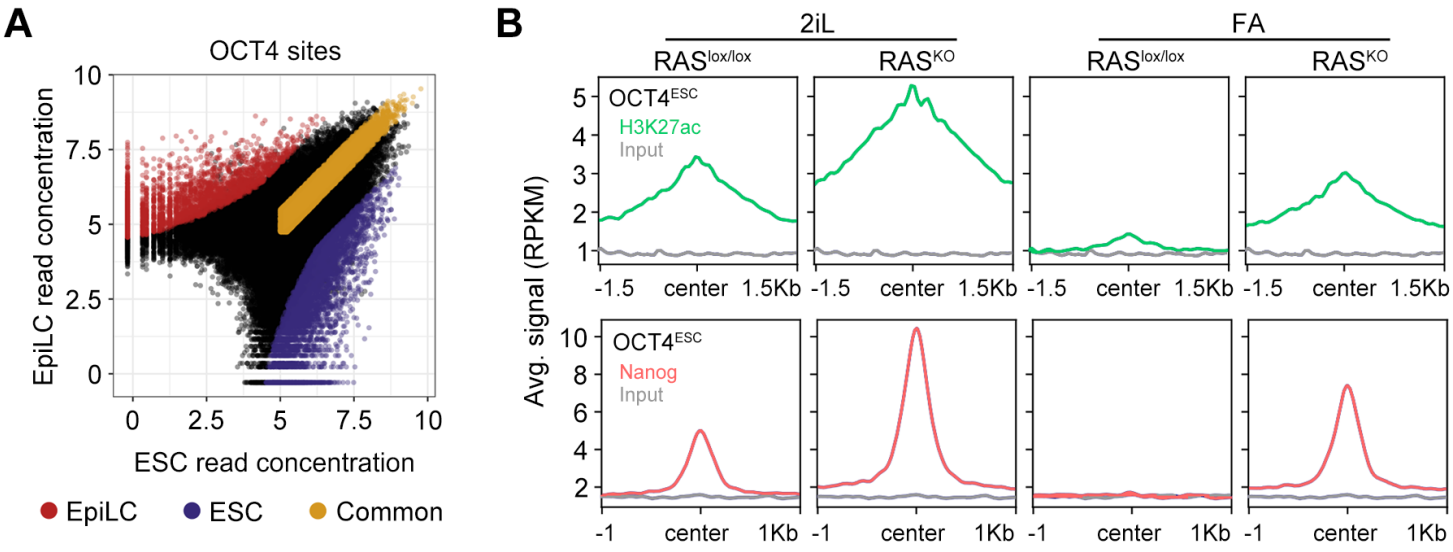
A
OCT4 sites
EpiLC read concentration
ESC read concentration
0
2.5
5
7.5
10
EpiLC
ESC
Common
B
2iL
FA
RASlox/lox
RASKO
RASlox/lox
RASKO
OCT4ESC
H3K27ac
Input
OCT4ESC
Nanog
Input
Avg. signal (RPKM)
-1.5
center
1.5Kb
-1
center
1Kb

**Figure S8**

**Figure S8: The naïve enhancer landscape is active in FA-RAS$^{KO}$ ESC.** (**A**) Classification of OCT4 sites based on change in occupancy during differentiation. Replicates of OCT4 peaks in ESC and EpiLC (*27*) were used to determine differentially bound peaks using DiffBind (*63*). A threshold of p-val<0.01 and FDR<0.03 and <2-fold read concentration was chosen to define ESC-specific sites (blue) and EpiLC-specific sites (red). A set of least-changed OCT4 peaks between was treated as common or shared sites (orange). (**B**) Cut&Run read density plot showing H3K27ac (plots above, green) and NANOG (plots below, red) occupancy in all OCT4$^{ESC}$ sites in RAS$^{lox/lox}$ and RAS$^{KO}$ cultured in 2iL or differentiated to EpiLC (FA). Corresponding inputs (IgG) are also shown as reference control.

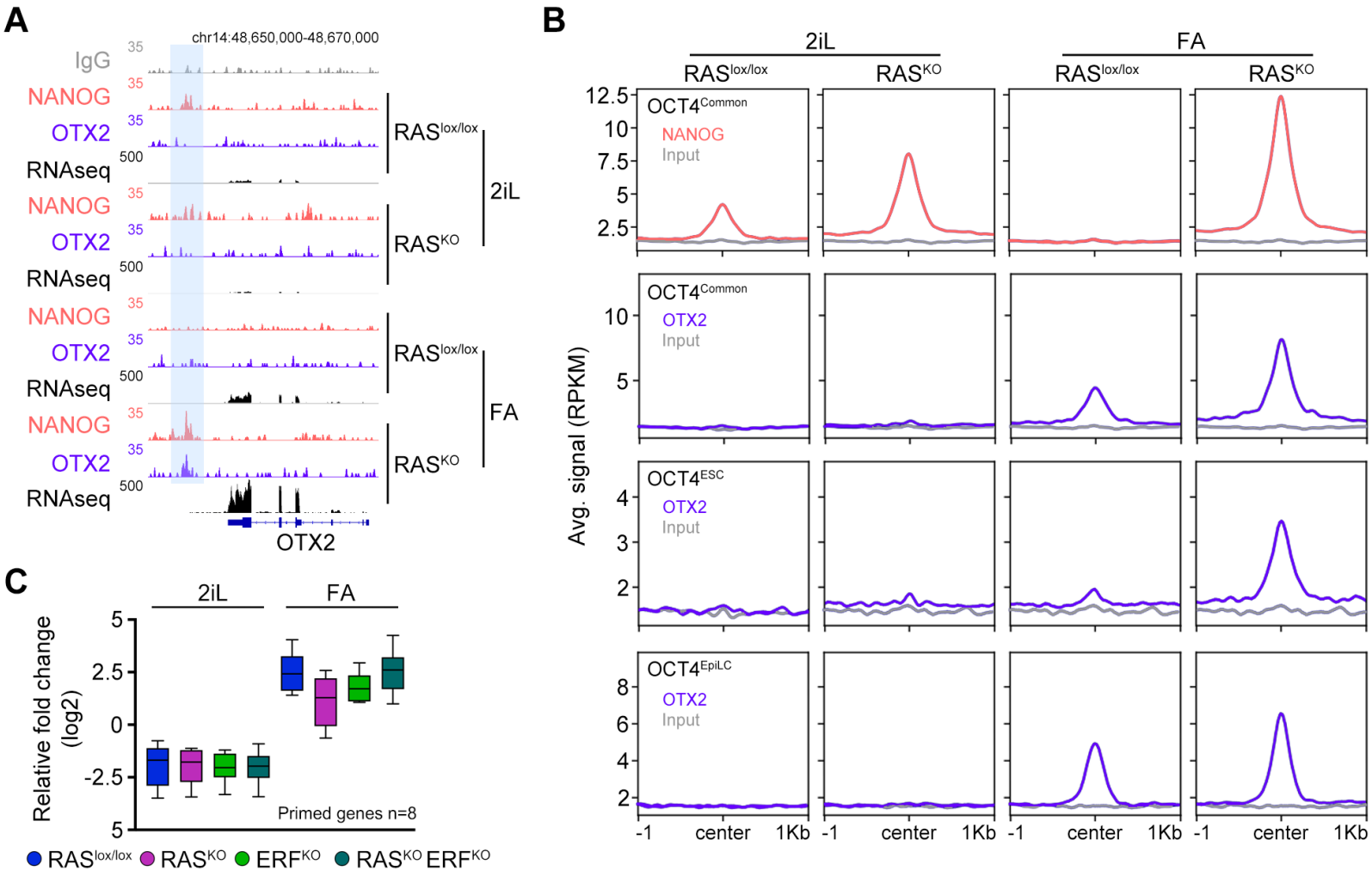
A
chr14:48,650,000-48,670,000
IgG
NANOG
OTX2
RNAseq
RASlox/lox
RASKO
2iL
FA
OTX2
B
2iL
FA
RASlox/lox
RASKO
OCT4Common
NANOG
Input
OTX2
OCT4ESC
OCT4EpiLC
Avg. signal (RPKM)
-1
center
1Kb
C
Relative fold change (log2)
Primed genes n=8
RASlox/lox
RASKO
ERFKO
RASKO ERFKO

**Figure S9**

**Figure S9: OTX2 co-occupies binding sites with NANOG in FA-RAS$^{KO}$ ESC.** (**A**) Genome browser tracks showing NANOG and OTX2 occupancy at the OTX2 gene and RNAseq RPKM read count in RAS$^{lox/lox}$ and RAS$^{KO}$ ESC cultured in 2iL or differentiated to EpiLC (FA). Inputs (IgG) are also shown as a reference control. Blue squares showed ERF binding sites. (**B**) Cut&Run read density plot showing NANOG (red) and OTX2 (purple) occupancy in the indicated OCT4$^{Common}$, OCT4$^{ESC}$ and OCT4$^{EpiLC}$ sites in RAS$^{lox/lox}$ and RAS$^{KO}$ ESC cultured in 2iL or differentiated to EpiLC (FA). Corresponding inputs (IgG) are also shown as reference control. (**C**) Graph showing the relative fold change (log2) expression of a subset of 8 genes associated to primed pluripotency (*Dnmt3a*, *Dnmt3b*, *Fgf5*, *Fgf15*, *OCT6*, *Wnt8a*, *Otx2* and *Dnmt3l*) in the different genotypes in 2iL or differentiated to EpiLC (FA). For each gene, data was normalized to the average across all samples.

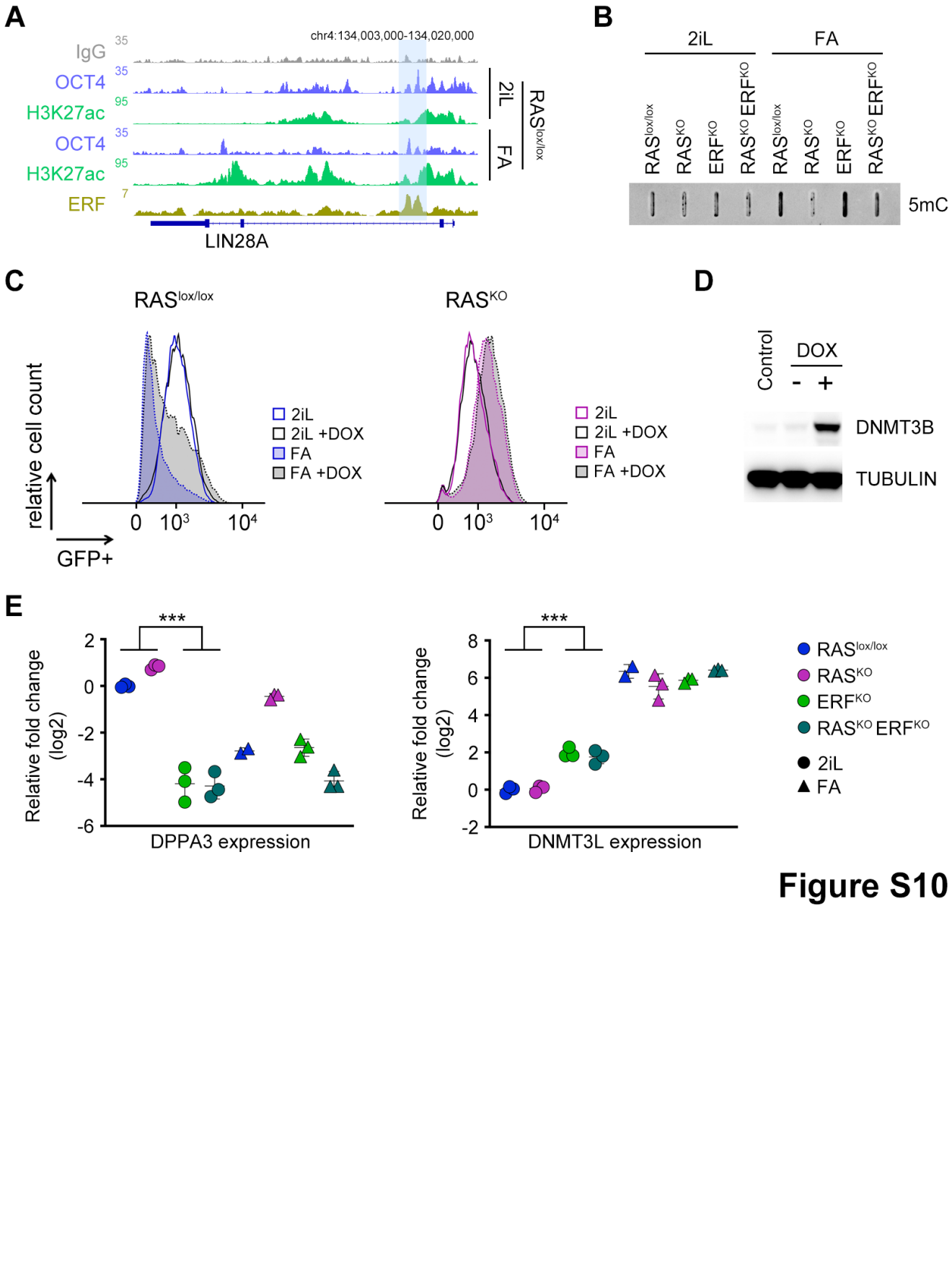
A
chr4:134,003,000-134,020,000
IgG
OCT4
H3K27ac
OCT4
H3K27ac
ERF
2iL
FA
RASlox/lox
LIN28A
B
2iL
FA
RASlox/lox
RASKO
ERFKO
RASKO ERFKO
5mC
C
RASlox/lox
RASKO
relative cell count
GFP+
2iL
2iL +DOX
FA
FA +DOX
D
Control
DOX
- +
DNMT3B
TUBULIN
E
***
Relative fold change (log2)
DPPA3 expression
DNMT3L expression
RASlox/lox
RASKO
ERFKO
RASKO ERFKO
2iL
FA

**Figure S10**

**Figure S10: ERF controls methylation during naïve-to-primed transition.** (**A**) Genome browser tracks showing H3K27ac deposition and OCT4 occupancy at the LIN28A gene in $RAS^{lox/lox}$ ESC cultured in 2iL or differentiated to EpiLC (FA). ERF binding profile in $RAS^{KO}$ ESC is also shown. Inputs (IgG) are also shown as a reference control. Blue squares showed ERF binding sites. (**B**) Dot blot analysis to detect the levels of 5mC in ESC from all genotypes cultured in 2iL or differentiated to EpiLC (FA). (**C**) Flow cytometry analysis of REX1-deGFP reporter ESC from $RAS^{lox/lox}$ and $RAS^{KO}$ ESC cultured in 2iL or differentiated for 48 hours to EpiLC (FA). ESC were untreated or 1μg/ml Doxycycline (DOX)-treated for the duration of the experiment (48 hours) to induce DNMT3B expression. Three independent experiments were performed but one representative experiment is shown. (**D**) Representative western blot analysis in $RAS^{KO}$ ESC cultured in 2iL untreated or 1μg/ml Doxycycline (DOX)-treated for 24 hours to demonstrated effective DNMT3B expression. (**E**) Plots showing the relative fold change (log2) expression for DPPA3 (left panel) and DNMT3L (right panel) in ESC from all genotypes cultured in 2iL or differentiated to EpiLC (FA). Data is shown as triplicates. For each gene, data was normalized to the average across all samples. *** = $p<0.001$, T-student.

**Table S1:** Primers used in this study.

| Oligonucleotides |
|---|
| Primer for left homology REX1 arm:<br>5'-REX1-KpnI-F: ACGTGGTACCTCTTTGCCTTACAGAGAAGCC |
| Primer for left homology REX1 arm:<br>5'-REX1-SacI-R: ACGTGAGCTCGTTGTCTTAGCTGCTTCCTTC |
| Primer for right homology REX1 arm:<br>3'-REX1-NotI-F: ACGTGCGGCCGCAGGTGGAGACAGATTGTCCTC |
| Primer for right homology REX1 arm:<br>3'-REX1-XhoI-F: ACGTCTCGAGTTGCCTTAAGTTCTGTATGC |
| eGFPd2-F: ACAACATGGTGAGCAAGGGCGAGGAGC |
| eGFPd2-R: ACGTCTACACATTGATCCTAGCAGAAG |
| sgRNA-REX1-F1: CACCGAGTGGCCAGAAAGGGCCGGG |
| sgRNA-REX1-R1: AAACCCCGGCCCTTTCTGGCCACTC |
| sgRNA-REX1-F2: CACCGCCATATCCGCATCCACACCG |
| sgRNA-REX1-R2: AAACCGGTGTGGATGCGGATATGGC |
| Primer for cloning DNMT3B in PB-TRE-dCas9-VPR:<br>5'-DNMT3B-NheI-F: GCTAGCTAGCACCATGAAGGGAGACAGCAGACATC |
| Primer for cloning DNMT3B in PB-TRE-dCas9-VPR:<br>3'-DNMT3B-PmeI-R: GCTAGTTTAAACTTCACAGGCAAAGTAGTCCTTC |

**Table S2:** Antibodies used in this study.

| ANTIBODIES | SOURCE | IDENTIFIER |
|---|---|---|
| ERF Antibody (E-9) | Santa Cruz Biotechnology | Cat# sc-398269 |
| Anti-Nanog antibody | Abcam | Cat# ab80892, RRID:AB_2150114 |
| Anti Nanog (Mouse) pAb | Cosmo Bio USA | Cat# REC-RCAB002P-F |
| Mouse KLF4 Antibody | R&D systems | Cat# AF3158, RRID:AB_2130245 |
| Mouse Podocalyxin Antibody | R&D systems | Cat# MAB1556, RRID:AB_2166010 |
| Human Otx2 Antibody | R&D systems | Cat# AF1979, RRID:AB_2157172 |
| Anti-Otx1 + Otx2 antibody | Abcam | Cat# ab21990, RRID:AB_776930 |
| Alexa Fluor™ 488 Phalloidin | Invitrogen | Cat# A12379 |
| Anti-OCT6 Antibody, clone KT110 | Millipore | Cat# MABN738, RRID:AB_2876862 |
| Human ERR beta/NR3B2 Antibody | R&D systems | Cat# PP-H6705-00, RRID:AB_2100412 |
| Anti-Sox2 Antibody | Millipore | Cat# AB5603, RRID:AB_2286686 |
| Anti-Sox2 (D9B8N) antibody | Cell Signaling | Cat# 23064S, RRID: AB_2714146 |
| Anti-Histone H3 (acetyl K27) antibody | Abcam | Cat# ab4729, RRID:AB_2118291 |
| p44/42 MAPK (Erk1/2) Antibody | Cell Signaling Technology | Cat# 9102, RRID:AB_330744 |
| Phospho-p44/42 MAPK (Erk1/2) (Thr202/Tyr204) Antibody | Cell Signaling Technology | Cat# 9101, RRID:AB_331646 |
| LIN28A (D1A1A) XP® Rabbit mAb | Cell Signaling Technology | Cat# 8641, RRID:AB_10997528 |
| LIN28B Antibody | Cell Signaling Technology | Cat# 5422, RRID:AB_10697489 |
| GATA6 Antibody | R&D systems | Cat# AF1700, RRID:AB_2108901 |
| Monoclonal Anti-α-Tubulin antibody | Sigma-Aldrich | Cat# T9026, RRID:AB_477593 |
| Anti-DNMT3B antibody | Abcam | Cat# ab122932, RRID:AB_10933207 |
| DNMT3A Antibody | Novus Biological | Cat# NB120-13888, RRID:AB_789607 |
| Pan-RAS (Ab-3) Mouse mAb (RAS 10) | Millipore | Cat# OP40-100UG, RRID:AB_213400 |
| Anti-5-methylcytosine (5-mC) antibody [33D3] | Abcam | Cat# ab10805, RRID:AB_442823 |
| Guinea Pig anti-Rabbit IgG (Heavy & Light Chain) Antibody | Antibodies-Online | Cat# ABIN101961, RRID:AB_10775589 |
| Goat anti-Rabbit IgG (H+L) Secondary Antibody, HRP | Thermo Fisher Scientific | Cat# 31466, RRID:AB_10960844 |

| | | |
|---|---|---|
| Goat anti-Mouse IgG (H+L) Secondary Antibody, HRP | Thermo Fisher Scientific | Cat# 31431, RRID:AB_10960845 |
| Chicken anti-Rabbit IgG (H+L) Cross-Adsorbed Secondary Antibody, Alexa Fluor 488 | Thermo Fisher Scientific | Cat# A-21441, RRID:AB_2535859 |
| Goat anti-Mouse IgG (H+L) Cross-Adsorbed Secondary Antibody, Alexa Fluor 568 | Thermo Fisher Scientific | Cat# A-11004, RRID:AB_2534072 |
| Donkey anti-Mouse IgG (H+L) Highly Cross-Adsorbed Secondary Antibody, Alexa Fluor 568 | Thermo Fisher Scientific | Cat# A10037, RRID:AB_2534013 |
| Chicken anti-Goat IgG (H+L) Cross-Adsorbed Secondary Antibody, Alexa Fluor 488 | Thermo Fisher Scientific | Cat# A-21467, RRID:AB_2535870 |
| Chicken anti-Rabbit IgG (H+L) Cross-Adsorbed Secondary Antibody, Alexa Fluor 647 | Thermo Fisher Scientific | Cat# A-21443, RRID:AB_2535861 |
| Donkey anti-Rabbit IgG (H+L) Highly Cross-Adsorbed Secondary Antibody, Alexa Fluor 568 | Thermo Fisher Scientific | Cat# A10042, RRID:AB_2534017 |
| Chicken anti-Rat IgG (H+L) Cross-Adsorbed Secondary Antibody, Alexa Fluor 488 | Thermo Fisher Scientific | Cat# A-21470, RRID:AB_2535873 |
| Chicken anti-Mouse IgG (H+L) Cross-Adsorbed Secondary Antibody, Alexa Fluor 647 | Thermo Fisher Scientific | Cat# A-21463, RRID:AB_2535869 |
| | | |

**Table S3:** Software and Algorithms used in this study.

| Software and Algorithms | | |
|---|---|---|
| Cut&RunTools | Zhu et al., 2019 (*59*) | https://bitbucket.org/qzhudfci/cutruntools/ |
| fastp v.0.20.0 | Chen et al., 2018 (*50*) | https://github.com/OpenGene/fastp |
| bowtie2 | Langmead et al., 2012 (*60*) | http://bowtie-bio.sourceforge.net/bowtie2/index.shtml |
| macs2 | Zhang et al., 2008 (*63*) | https://github.com/macs3-project/MACS |
| deepTools | Ramirez et al., 2016 (*54*) | https://github.com/deeptools/deepTools |
| Picard toolkit | | http://broadinstitute.github.io/picard/ |
| phantompeakqualtools | Kharchenko et al., 2008 (*61*) | https://github.com/kundajelab/phantompeakqualtools |
| Diffbind v3.0.5 | Stark R. and Brown G. D. (2011) (*64*) | https://bioconductor.org/packages/release/bioc/html/DiffBind.html |
| trimgalore v0.6.5 | | http://www.bioinformatics.babraham.ac.uk/projects/trim_galore |
| Bismark v0.22.1 | Krueger et al., 2011 (*65*) | https://github.com/FelixKrueger/Bismark |
| methylKit v1.14.2 | Akalin et al., 2012 (*66*) | https://bioconductor.org/packages/release/bioc/html/methylKit.html |
| Prism 8 | GraphPad | https://www.graphpad.com/ |
| FlowJo (10.1) | FlowJo LLC | https://www.flowjo.com/ |
| DNAnexus | DNAnexus | https://www.dnanexus.com/ |
| IGV | | https://igv.org/ |
| R (3.5 and 4.0) | | www.r-project.org |
| GREAT | | http://great.stanford.edu/public/html/ |
| DESEQ2 | Love et al., 2014 (*52*) | http://bioconductor.org/packages/release/bioc/html/DESeq2.html |
| Imaris Bitplane | Oxford Instruments | https://imaris.oxinst.com/ |